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The Biological Half-life of Inorganic Mercury in the Dungeness Crab (*Cancer magister*)

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SLOAN, J. P., J. A. J. THOMPSON, AND P. A. LARKIN. 1974. The biological half-life of inorganic mercury in the Dungeness crab (*Cancer magister*). J. Fish Res. Board Can. 1571–1576.

The biological half-life of inorganic mercury in the Dungeness crab, *Cancer magister*, has been determined experimentally to be about 25 days. Three theoretical models to explain the mode of elimination were tested by computer program. From results obtained, the validity of the widely used negative exponential "biological half-life" is left in some doubt.

SLOAN, J. P., J. A. J. THOMPSON, AND P. A. LARKIN. 1974. The biological half-life of inorganic mercury in the Dungeness crab (*Cancer magister*). J. Fish Res. Board Can. 1571–1576.

Nous avons établi expérimentalement à environ 25 jours la demi-vie biologique du mercure inorganique dans le dormeur du Pacifique, *Cancer magister*. A l'aide d'un programme d'ordinateur, nous avons mis à l'épreuve trois modèles théoriques pour expliquer le mode d'élimination. Les résultats obtenus font douter quelque peu de la validité de la «demi-vie biologique» à exposant négatif si souvent employée.

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Methods

HOLDING AND DOSING

For clearing rate experiments, mature specimens of *Cancer magister* were obtained commercially from Boundary Bay, B.C. For each experiment 60 crabs were maintained in captivity; 50 were exposed simultaneously to dissolved inorganic mercury in aquarium water, returned to unpolluted sea water in the original aquarium, and then analyzed for total mercury content in groups of four at various time intervals after exposure. Several large (1.8 m diameter, 1.2 m depth) outdoor cylindrical fiberglass aquaria were used to accomplish this.

Each aquarium used for holding crabs before and after dosing was fitted with a central double concentric standpipe with outlets in the outer pipe at the bottom

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(for maximum circulation) and length of the inner pipe (approximately 0.5 m) set to maintain constant depth. Water taken from Burrard Inlet entered from a pipe trained obliquely to the aquarium at a rate that provided a complete water change every 10–15 min. Water flow also caused a slow, clockwise circulation in each aquarium; aeration was supplemented by an airstone. During the experiments, salinity (average 28‰) and temperature (average 10 C) showed only mild seasonal variation.

During dosing, (2 h), a closed system was maintained in which the outlet of the center of the dosing aquarium and another near its perimeter were each fitted with a rubber hose through which water was drained, and recycled over the top of the aquarium by two electric pumps.

Aside from sampling periods, all crabs were left undisturbed throughout the program, and were fed with herring to satiation.

A standard dosing procedure was followed throughout the program. On the day before exposure, 10 crabs were selected and marked as controls. On the day of treatment, the dosing aquarium was fitted as described above and a weighed amount of mercuric nitrate (J. T. Baker Reagent), dissolved in about 1 liter water, was added to the recirculated aquarium water. The 50 unmarked crabs were then quickly transferred from the holding aquarium and left undisturbed in the dosing aquarium for the 2-h exposure.

Five experiments were performed. Experiment 1 and 5 were performed at nominal concentrations of 10 ng Hg^{2+}/ml while numbers 2, 3, and 4 were with nominal concentrations of 500 ng Hg^{2+}/ml of dosing water. Five replicate analyses of the dosing medium were performed for each experiment. Ranges and standard deviations for each were as follows: 1) 10–15 ± 2.2 ng/ml, 2) 443–557 ± 49 ng/ml, 3) 410–460 ± 21 ng/ml, 4) 482–541 ± 25 ng/ml, and 5) 7–12 ± 2.2 ng/ml. Some loss in accuracy of dosing was incurred in working with the large volume of water in the dosing aquarium.

Values for the half-time were calculated using the formula:

$$T_{\frac{1}{2}} = \frac{(C_0 - \bar{B})}{2\ R} \qquad (1)$$

where $T_{\frac{1}{2}}$ is the biological half-time; R is the rate of release, as determined by a least-squares line of best fit to the data; C_0 is the initial body content after dosing, as determined by the Y-intercept of the line of best fit; $\bar{B}$ is the average background body content, i.e. the mean body content of all control animals.

Estimates of R and C_0 were in each case obtained by regression of the difference between treatment and mean control value against time.

TABLE 1. Mean[a] body content of mercury in Dungeness crab (*Cancer magister*) tissue homogenates at time after dose (Experiment 4). Mean control 74 (± 36) ng/g.

Time (*h*)	Hg (*ng/g*)	SD
1	758	228
18	611	141
42	535	103
72	566	65
165	484	107
264	377	87
408	447	59
840	291	70

[a]Mean for four animals (wet weight).

Analysis

Animals selected for analysis were sacrificed by a sharp midventral blow. All tissue except the exoskeleton and gastrointestinal tract was dissected out and homogenized (Sorval Omnimixer), and the homogenate was covered to avoid evaporation and contamination. Digestion of tissue for total mercury determination was similar to that described by Armstrong and Uthe (1971). Initial tissue breakdown with a sulphuric acid–nitric acid mixture (J. T. Baker low-mercury reagents) was followed by incubation in 6% $KMnO_4$ and decolorization with 50% H_2O_2. A modification of the method involved a back-titration with $KMnO_4$ to a slight pinkness to ensure oxidizing conditions in the solution. Flameless mercury analysis was performed using a Perkin–Elmer Model 403 Atomic Absorption Spectrophotometer fitted with cold-vapor apparatus similar to that described by Manning (1970).

Results

The expected decline in mercury body burden was observed in all experiments (Table 1, Fig. 1).

Semilogarithmic and linear treatments of the data (Fig. 1 and 2) yielded mean half-time values differing by about 5 days, the semilog derivation providing the lower of the two (Table 2).

The second question (whether a simple negative exponential relation is qualitatively adequate for describing the release of mercury from *C. magister*) was approached by evaluation of linear and nonlinear components of least-squares lines of best fit. This procedure was used to evaluate both an arithmetic time vs. arithmetic body content line form and a log time vs. log content form (Fig. 2a, b) as well as the semilogarithmic form. (Fig. 1). Table 3 shows the results of this analysis expressed as probabilities that the line of best fit is an adequate

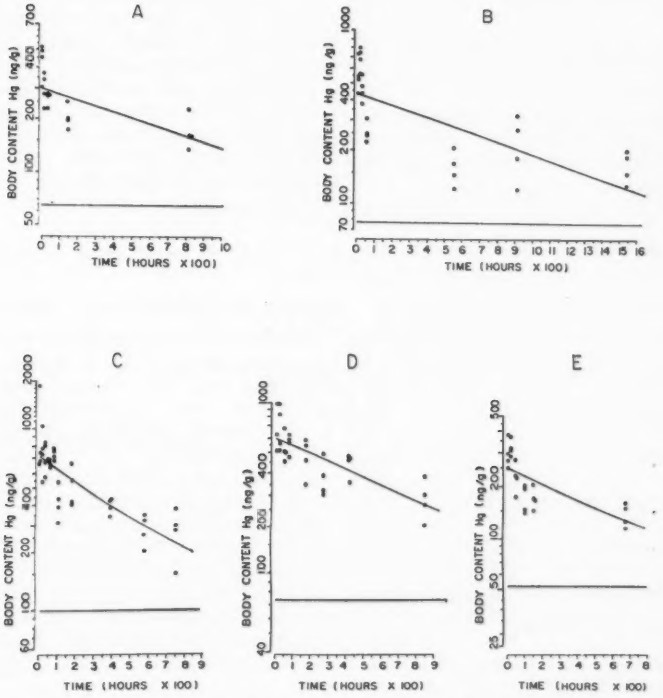

FIG. 1. Relation between log body content of Hg (ng/g) and time in Dungeness crabs (*Cancer magister*) exposed to Hg solutions. A–E, experiments 1–5 respectively.

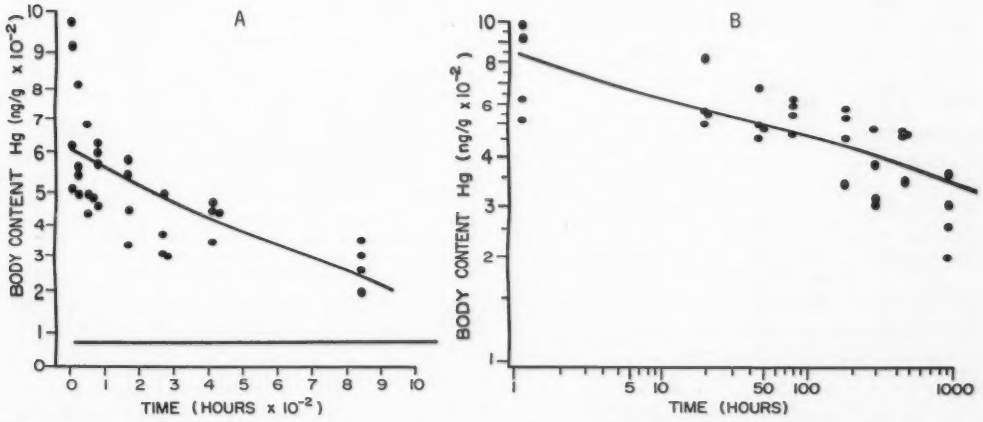

FIG. 2. Graphical representation of data from experiment 4. A, arithmetic body content vs. arithmetic time; B, log body content vs. log time.

description of the relation between time and body content.

The inadequacy of any of the three simple line forms in describing the relation, led to the idea that the clearing rate might be the result of multiple events, which might not in themselves be complex. Specifically, it seemed possible that two or more sources of mercury existed in the animal and that the clearing rate from each source might be different. Further, the relatively fast initial clearing rates and relatively slow subsequent ones suggested two concurrent processes, each with a simple negative exponential clearing rate. Equation 2 shows a model conceived to test this idea.

TABLE 2. Experimentally determined biological half-life (days) of inorganic mercury in *C. magister* for arithmetic and semilogarithmic regressions of mercury content against time.

	Arithmetic		Semilogarithmic	
Experiment	Half-life	SD	Half-life	SD[a]
1	27.1	9.1	20.5	+6.7 −4.0
2	32.9	7.3	18.0	+4.4 −2.9
3	18.3	3.6	14.6	+2.1 −1.5
4	24.4	5.2	30.8	+6.0 −4.5
5	21.7	5.7	17.7	+4.6 −3.0
Mean	24.9		20.3	

[a]Two values of the semilogarithmic standard deviation correspond to equal log intervals.

TABLE 3. Probability that there is no significant departure from linearity in regression. Axes are indicated as follows: A, arithmetic body content vs. arithmetic time; B, logarithmic body content vs. arithmetic time; C, logarithmic body content vs. logarithmic time.

Axes	Experiment	Probability of validity
A	1	0.00043
	2	0.00001
	3	0.15201
	4	0.09665
	5	0.00013
B	1	0.00128
	2	0.00005
	3	0.10295
	4	0.18025
	5	0.00029
C	1	0.93413
	2	0.01884
	3	0.02484
	4	0.15076
	5	0.00710

$$Hg_T = Hg_o\,[P_1e^{-K_1T} + (1-P_1)e^{-K_2T}] \qquad (2)$$

where Hg_o is initial body content Hg.

P_1 is the proportion of the total Hg in the first concurrent process, K_1 is the rate of release from the first concurrent process, and K_2 is the rate of release from the second concurrent process.

A program, MARQD (Marquardt 1963), to estimate parameters for nonlinear systems such as this one, was applied for Equation 2 to the data from all five experiments. Table 4 shows the best parameters derived by this program, and the percent variance explained by each set of parameters.

A modification to Equation 2, which would allow a proportion Q of the mercury released by the first concurrent process to be recycled into the second concurrent process and then released at a rate of K_2 (Equation 3), was also tested.

$$Hg_T = Hg_o\,[P_1e^{-K_1T} + (1-P_1)e^{-K_2T} + QP_1(1-e^{-K_1T})e^{-K_2T}] \qquad (3)$$

The parameters derived for this model by two calls to the MARQD program, are shown in Table 5.

It is clear from the large residual variability for the simple negative exponential relation of body content to time, that values for biological half-time (calculated using that line form) are useful only as approximations.

The concurrent processes models (Equation 2 and 3) also remain unsubstantiated by the statistical

TABLE 4. Estimated parameters for concurrent processes model (Equation 2).

Experiment	P_1	K_1	K_2	% Variance explained
1	0.51481	0.00040	0.09044	77.69
2	0.74733	0.02696	0.00003	81.35
3	0.65209	0.00128	0.06527	53.34
4	Convergence not achieved			
5	0.43778	0.00006	0.01408	73.12

TABLE 5. Estimated parameters for concurrent processes model with recycling (Equation 3).

Experiment	Call	P_1	K_1	K_2	Q	% Variance explained
1	1	0.51480	0.00040	0.09017	0.58392	77.69
	2	37.830[a]	0.00023	0.00058	1.8443[a]	59.86
2	1	0.83745	0.00084	0.00559	20.487[a]	83.92
	2	0.83768	0.00084	0.00559	20.478[a]	83.92
3	1	0.65207	0.00128	0.06460	0.27364	53.34
	2	0.65209	0.00128	0.06467	0.26844	53.35
4	1	0.01169	0.06732	0.00079	23.407[a]	59.09
	2	0.01234	0.06730	0.00077	22.124[a]	59.09
5	1	0.45727	0.00000	0.01055	959.67[a]	73.17
	2		Convergence not achieved			

[a]Indicates nonsense estimate.

tests applied to them, although a fairly large percentage of the variation is explained by those models in many cases. The recycling model showed nonsense values for best estimates, by MARQD, of some of its parameters, and without independent evidence as a basis for constraining some of the variables it was not possible to evaluate the validity of the model assumption.

Discussion

The experimental data derived from the five experiments indicate that inorganic mercury has a biological retention time of about 20–25 days, depending on the mode of mathematical deviation (Table 2). This is a value that is similar to those for ^{203}Hg (as the chloride) of 5–10 days in the mollusc, *Tapes decussatus* (Ünlü et al. 1972), and to the third and fourth components of the decay period in the Pacific oyster, *Crassostrea gigas* (Seymour 1971). In all cases, half-life values for Hg^{2+} are far less than those determined for methylmercuric species (Jarvenpää et al. 1970; Miettinen et al. 1972).

The use of labelled mercury in half-life determinations predominates in the literature. In the present work, the inexpensive and considerably less involved atomic absorption method was used. There is, to our knowledge, no precedent for biological half-life determination by this method.

The models were conceived to explain the results on the following basis: it was thought that two concurrent systems could exist in one or more of several physical situations. Release of mercury from two different tissues (e.g. liver and muscle) might occur at different but intrinsically consistent rates, perhaps due to differences in protein content in the tissues. Further models could be almost infinitely extended to include other tissues.

Two chemical forms of mercury might express different affinities for tissue in different rates of release.

In either case, mercury could leave the pool of the faster concurrent process to enter that of the slower one. It is conceivable that the pool of the slower process might hold a greater amount of mercury at some time after dosing than it does immediately following exposure.

Finally, another hypothesis (not tested by a model here) that would explain a fast initial clearing rate and a slow later one, is degenerative pathological change. Destruction, or blocking of enzyme pathways, in excretory organs could lead to progressively reduced ability to eliminate free mercury, which would then recycle into the organisms.

The doubts raised by the results obtained here as to the validity of the widely used negative exponential "biological half-time" in *C. magister*, has led to the speculation that similar doubts could be raised if other species and other foreign materials were examined closely. It seems reasonable to assume that the interface of living tissue and nonliving, external material may often be complicated by variation in form, whether of the tissue or the material, or by pathological changes caused by the material. It may also be that in studying the mechanisms of uptake, binding, and release, when these are of interest, hypotheses could be conveniently tested with models and line-form analysis similar to those we have used here.

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Lipids of Zooplankton from Bute Inlet, British Columbia

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LEE, R. F. 1974. Lipids of zooplankton from Bute Inlet, British Columbia. J. Fish Res. Board Can. 31: 1577–1582.

Seventeen species of zooplankton representing four phyla were collected from Bute Inlet, one of the deep inlets (650 m) in British Columbia. Using lipid analysis and starvation studies, the zooplankton were divided into two categories based on whether the level of storage lipid was high or low. The polychaetaes, chaetognaths, and one of the ctenophores (*Pleurobrachia pileus*) were characterized by little storage lipid (neutral lipid only 7–10% of the lipid). It is assumed that these species transfer most new organic matter into new tissue rather than storage lipid. The copepods, *Calanus plumchrus*, *Eucalanus bungi*, *Gaetanus columbiae*, and *Heterorhadus tanneri*, were all characterized by high levels of storage lipid (between 53 and 90% of the lipid) and, except for *Eucalanus*, these consisted mainly of wax esters. The remaining zooplankters (ostracods, pteropods, euphausiids, amphipods, and decapods), except for the ctenophore, *Beroe cucumis*, stored primarily triglycerides. In all species examined, except *B. cucumis*, five fatty acids, 16:0, 16:1, 18:1, 20:5, and 22:6, accounted for over 90% of the total phospholipid fatty acid complement. Polyunsaturated C_{16} and C_{18} acids, which are common in phytoplankton, were absent or present in trace amounts in phospholipids but were abundant in the neutral lipids of herbivorous zooplankton. The wax esters of *G. columbiae* and *B. cucumis* had high levels of 16:0, 20:1, and 22:1 alcohols, whereas *C. plumchrus* had only 20:1 and 22:1 alcohols as major components.

LEE, R. F. 1974. Lipids of zooplankton from Bute Inlet, British Columbia. J. Fish. Res. Board Can. 31: 1577–1582.

Nous avons récolté dans l'inlet Bute, un des inlets profonds (650 m) de la Colombie-Britannique, 17 espèces de zooplancton, représentant quatre embranchements. L'analyse des lipides et des études de jeûne nous ont permis de diviser le plancton en deux catégories, selon le niveau, élevé ou bas, des lipides de stockage. Les polychètes, chétognathes et un des cténophores (*Pleurobrachia pileus*) sont caractérisés par un faible niveau de lipides de stockage (lipides neutres seulement 7–10% des lipides). On suppose que ces espèces transfèrent la plus grande partie de la matière organique nouvelle à du tissu nouveau plutôt qu'à des lipides de stockage. Les copépodes, *Calanus plumchrus*, *Eucalanus bungi*, *Gaetanus columbiae* et *Heterorhadus tanneri*, sont tous caractérisés par de hauts niveaux de lipides de stockage (entre 53 et 90%) des lipides qui, sauf chez *Eucalanus*, consistent surtout en esters de cire. Les autres animaux planctoniques (ostracodes, ptéropodes, euphausides, amphipodes et décapodes), à l'exception du cténophore *Beroe cucumis*, emmagasinent surtout des triglycérides. Chez toutes les espèces examinées, sauf *B. cucumis*, cinq acides gras, 16:0, 16:1, 18:1, 20:5 et 22:6 constituent plus de 90% du complément total acides gras des phospholipides. Les acides polyinsaturés C_{16} et C_{18}, communs dans le phytoplancton, sont absents ou présents à l'état de traces dans les phospholipides, mais sont abondants dans les lipides neutres du zooplancton herbivore. Les esters de cire de *G. columbiae* et de *B. cucumus* ont des niveaux élevés des alcools 16:0, 20:1, et 22:1 alors que *C. plumchrus* n'a, comme composants majeurs, que les alcools 20:1 et 22:1.

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BUTE Inlet is a deep fjord (650 m) of British Columbia, characterized at its head by a series of glaciers that create a plume of fresh water. An unusual occurrence in this inlet is the formation of large amounts of a waxy material, the so-called "Bute Inlet Wax," composed largely of wax esters. The hypothesis that zooplankton, specifically copepods, are the source of this wax has been presented in an earlier report (Benson et al. 1972; Nevenzel et al. 1971).

The present work gives the results of lipid analyses of 17 species of zooplankton, belonging to four phyla, that were collected during several cruises to the inlet. Besides determining the type and amount of storage lipid for each species, the fatty

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acids and alcohols of different lipid classes from some species were analyzed. The fatty acids of the storage lipids, i.e. wax esters and triglycerides, should reflect dietary fatty acids, and the presence of a high proportion of polyunsaturated C_{16} and C_{18} acids could be due to phytoplankton in the diet. Of special interest was the possible presence of wax esters in zooplankton, other than copepods. Wax esters are a class of neutral lipids composed of a fatty acid esterified to a long chain alcohol. Earlier work has shown that these are the predominant lipid of many temperate water copepods (Lee et al. 1972) and serve as reserve fuels.

Materials and Methods

Plankton tows were made in Bute Inlet at several depths using open nets of 0.505-mm mesh on cruises of the R/V *Dolphin* and the Canadian Hydrographic Service Ship *Vector* during May, September, and October. Live zooplankton were sorted from the samples into homogenous groups of species and developmental stages. Some individuals of each group were preserved for identification; the remainder were used for lipid extraction. The paper by Fulton (1968) and the references cited herein were used for the identification of zooplankton.

Some species were maintained alive to study the rate of lipid utilization during conditions of "starvation." These zooplankton were kept in 2–5 liters of sea water at 8 C that had been passed through a 0.45-μ filter (Millipore Co.).

Lipid extraction was in chloroform–methanol (2:1 v/v). After extraction all work was carried out under nitrogen. The remaining dried carcasses were weighed to determine total dry weight. The extracted lipid was weighed and fractionated on a silicic acid column, eluting the different lipid classes with solvents of increasing polarity (Nevenzel et al. 1965). The phospholipid fraction was assayed for phosphorus (Rouser et al. 1966) and the sterol fraction for cholesterol (Kabara 1957). Procedures for analyzing wax esters, triglycerides, and phospholipids by gas–liquid chromatography are given in an earlier paper (Lee et al. 1971).

A Varian-Aerograph (series 1800) gas chromatograph equipped with a digital printout for peak areas was used for analytical determinations. This was equipped with two columns, a 2.4-mm × 3.2-mm (outside diameter) column of 10% SP-2100 on 100/120 Supelcoport and a 2.1-m × 3.2-mm column of 19% SP-222-PS on 100/120 Supelcoport (both supplied by Supelco, Inc., Bellefonte, Pa.). Temperature was programmed: methyl esters of fatty acids were run from 160 to 220 C on SP-2100 and from 180 to 190 C on SP-222; trifluoroacetate derivatives of long-chain alcohols from 160 to 220 C on SP-2100 and from 150 to 190 C on SP-222. Fatty acid and alcohol mixtures were also hydrogenated to aid in identifications. Authentic fatty acids and alcohols were used for identification. (A shorthand notation will be used throughout the text in referring to fatty acids and alcohols; for example, 20:5 refers to a molecule 20 carbon atoms long, with 5 double bonds.)

When less than 6 mg of total lipid was available the lipids were separated by silicic acid thin-layer chromatography and the amounts of wax esters and triglycerides determined spectrophotometrically by the procedure of Armenta (1964) using dichromate digestion and measurement at 350 nm.

The procedures used to separate, identify, and quantify phospholipids were those described by Parsons and Patton (1967) using thin-layer chromatography and phosphorus analysis.

Results

Most of the 17 species of zooplankton which were analyzed for lipid (Table 1) are common throughout the Strait of Georgia. The lipid content expressed as percent of dry weight varied from 9% in the ctenophore, *Pleurobrachia pileus*, to 47% in the copepod, *Calanus plumchrus*. All the copepods had a large visible oil sac which wax reflected in the high lipid content and, except for *Eucalanus bungii* with high triglyceride content, wax esters were the principal lipid class. Triglycerides were the main storage lipid in other zooplankton, except in the ctenophores, *Beroe cucumis* and *Pleurobrachia pileus*, and the chaetognath, *Sagitta elegans*, where triglyceride and wax ester were approximately in equal proportion (2–12% of the lipid). Besides the copepods, the other zooplankton which had large stores of neutral lipid were *Clione limacina* (pteropod), *Euprimno abyssalis* (amphipod), *Euphausia pacifica* juveniles, and *Pasiphaea pacifica* (decapod). The pteropod, *Clione limacina*, had triglyceride as the principal neutral lipid but glyceryl ethers were also an important lipid component accounting for 19% of the lipid. The glyceryl ethers were identified by behavior on thin-layer chromatography before and after acid hydrolysis and by infrared spectra (R. F. Lee unpublished data).

We attempted to maintain some animals in filtered sea water to determine if the animals could withstand long periods of starvation and to observe the rate of lipid utilization during starvation. All the copepods could be starved for a month (mortality was 10–20%). In *Heterorhadus tanneri*, *Gaetanus columbiae*, and *Calanus plumchrus* triglycerides were absent after this period, but at least 70% of the wax esters were still present. *Eucalanus bungii* had used some triglycerides but 40% remained. The chaetognath, *S. elegans*, and the ctenophores, *B. cucumis* and *P. pileus*, could be maintained for only 48 h at concentrations of one animal per 5 liters sea water. As after 12 h the animals appeared healhty we feel that starvation was the cause of death although other contributing factors, e.g. injury in collecting, cannot be ignored. Both *P. pileus* and

S. elegans had copepods in their guts when caught and they could be fed the copepod, *C. plumchrus*, in the laboratory. The digestion of copepods by *P. pileus* and *S. elegans* was followed as these are transparent carnivores. The oil from the copepods was released during the digestive process but within a few minutes the oil had disappeared. Because of the high rate of growth by *Pleurobrachia* (Hirota 1972) and *Sagitta* (Reeve 1970) and the lack of appreciable neutral lipid, even when feeding was intensive, we assume most oil was converted into protein.

The pteropod, *Clione limacina*, had 50% mortality for the first week of starvation but those remaining were maintained in the filtered sea water for 3 mo. At this time all the animals appeared healthy and would vigorously swim when disturbed. In 3 mo the lipid had decreased from 4.4 mg to 0.6 mg per individual due to utilization of glyceryl ethers, triglycerides, and wax esters. The ability of *C. limacina* to undergo long periods without food has been noted by Conover and Lalli (1972).

The fatty acids and fatty alcohols were analyzed in eight of the zooplankton species (Table 2). The polyunsaturated content of the phospholipids, due primarily to a high proportion of 20:5 and 22:6 fatty acids, was always higher than either triglycerides or wax esters. Five fatty acids, 16:0, 16:1, 18:1, 20:5, and 22:6, accounted for over 80% of the total phospholipid fatty acid complement in all species, except *Beroe cucumis*. In *B. cucumis* these acids accounted for 66% of the total phospholipid due to higher levels of 14:0 (17%) and 18:0 (11%) acids. The polyunsaturated C_{16} and C_{18} acids, primarily 16:2, 16:3, 16:4, 18:3, and 18:4, which are abundant in phytoplankton, were absent in zooplankton phospholipids, but one or more were important in the neutral lipids of *C. plumchrus*, *E. bungii*, and *E. pacifica*. This probably reflects phytoplankton in the diet. The principal alcohols of the wax esters in *C. plumchrus*, *G. columbiae*, and *B. cucumis* were 20:1 and 22:1 plus 16:0 in *B. cucumis* and *G. columbiae*. The 20:1 fatty acid was an important component of the triglycerides and wax

TABLE 1. Lipid of zooplankton from Bute Inlet.

Species	Lipid per individual (*mg*)	Lipid (% *dry wt*)	Wax ester (% *lipid*)	Triglyceride (% *lipid*)	Phospholipid (% *lipid*)
Annelida					
Nereis pelagica	8.1	–	T*	8	86
Glycera glycera	190	–	T	7	68
Tomapteris septentrionalis	–	22	T	7	82
Arthropoda					
Amphipoda					
Euprimno abyssalis	0.9	26	12	38	3
Hyperia galba	1.2	19	8	26	51
Copepoda					
Calanus plumchrus	0.48	47	86	4	4
Eucalanus bungii	0.12	40	11	75	8
Gaetanus columbiae	0.08	28	42	11	39
Heterorhadus tanneri	0.13	43	69	9	12
Decapoda					
Pasiphaea pacifica	41	21	4	65	22
Ostracoda					
Conchoecia elegans	0.04	17	4	27	65
Euphausiacea					
Euphausia pacifica	2.3	19	1	17	75
Euphausia pacifica juveniles	0.8	26	4	41	42
Chaetognatha					
Sagitta elegans	0.3	14	6	4	81
Ctenophora					
Beroe cucumis	7.4	13	12	8	69
Pleurobrachia pileus	0.3	9	6	2	73
Mollusca					
Clione limacina	4.4	31	4	32	31

*T, trace (less than 0.5%).

TABLE 2. Long-chain alcohols and fatty acids of zooplankton from Bute Inlet. Amounts expressed as weight percent.[a]

	G. columbiae				*C. plumchrus*				*B. cucumis*													
	WE				WE				WE				*E. bungii*		*C. elegans*		*E. pacifica* (juveniles)		*E. abyssalis*		*P. pacifica*	
Component[b]	Alc	FA	TG	PL	Alc	FA	TG	PL	Alc	FA	TG	PL	TG	PL	TG	PL	TG	PL	TG	PL	TG	PL
14:0	10	4	5	2	1	11	8	3	3	9	5	17	6	1	4	T	9	1	9	1	3	2
16:0	20	32	13	33	5	12	18	12	16	7	18	28	22	20	12	13	18	13	15	19	14	20
16:1	3	T	11	3	7	8	10	11	2	8	12	2	20	6	16	13	13	3	13	2	7	5
16:2	–	–	1	–	–	2	1	–	–	–	1	–	T	–	–	–	8	–	T	–	–	–
16:3	–	–	9	–	–	3	7	–	–	7	9	–	1	–	–	–	13	–	T	–	–	–
16:4	–	–	–	–	–	5	3	–	–	T	1	–	10	–	–	–	4	–	4	1	–	–
18:0	4	T	1	6	1	T	7	2	2	2	2	11	1	5	4	3	1	2	T	1	2	2
18:1	2	37	22	18	5	3	8	11	3	21	19	12	12	12	26	20	12	14	30	20	35	36
18:2	–	3	T	T	–	T	T	4	–	2	6	1	3	1	2	T	T	T	1	1	1	T
18:3	–	–	T	–	–	1	T	–	–	1	–	T	T	–	–	–	T	T	–	–	–	–
18:4	–	–	T	–	–	7	3	–	–	2	–	–	2	–	–	–	5	–	–	–	–	–
20:1	22	11	9	1	33	14	6	3	27	11	6	1	T	1	8	1	T	1	7	3	10	4
20:4	–	T	T	T	–	T	T	1	–	T	1	T	1	2	1	1	1	1	T	1	T	1
20:5	–	9	16	11	–	21	17	19	–	13	16	13	17	27	15	19	8	42	12	25	9	14
22:1	31	–	2	–	44	9	–	–	40	12	–	–	–	T	3	T	–	–	–	–	5	T
22:5	–	–	2	1	–	T	1	T	–	T	–	T	T	T	1	1	–	T	T	T	1	T
22:6	–	1	3	20	–	2	2	25	–	3	3	11	1	18	6	24	1	16	3	22	6	10
24:1	6	–	–	–	1	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–

[a]Abbreviations used: TG, triglycerides; WE, wax ester; FA, fatty acid; Alc, alcohol; PL, phospholipid; T, trace (less than 0.5%).
[b]Notation used for number of carbons followed by number of double bonds.

esters of these same species, but 22:1 fatty acid was important only in wax esters of *B. cucumis* and *C. plumchrus*. In the phospholipids 22:1 was absent and 20:1 was a minor component.

The principal phospholipids of all zooplankton examined were phosphatidyl choline (40–68%) with lesser amounts of phosphatidyl ethanolamine (19–30%). Minor components accounting for between 2 and 8% of phospholipid were cardiolipin, phosphatidyl inositol, and sphingomyelin. *Beroe cucumis* was unusual in that the phospholipids included 14% lysophosphatidyl choline. In the other species this lipid was less than 1% of the phospholipid.

Discussion

The zooplankton from Bute Inlet appear to fall into two categories: those that turn excess food into storage lipid, and those that use most food for new tissues. As most zooplankton examined to date are low in carbohydrate (Ikeda 1971; Raymont et al. 1969, 1971) and protein is assumed not to have an energy storage function, we speculate that low levels of neutral lipids are associated with zooplankton of category 2 which require constant feeding. The polychaetes may fall in this category based on their low lipid content. Both the ctenophore, *Pleurobrachia pileus*, and the chaetognath, *Sagitta elegans*, which were low in neutral lipids, could be starved only for 48 h. The present data supports the earlier work (Lee et al. 1972) that copepods of this temperate area are characterized by high levels of wax esters, whereas most other category 1 zooplankton stored lipid as triglycerides.

The phospholipids are viewed as having a structural role (i.e. components of membranes), and the phospholipid composition, with respect to both types and fatty acids, shows little variation within a zooplankton species regardless of changes in the quantity or type of food (Lee et al. 1971; R. F. Lee unpublished data). The same result was seen with oysters when fed different algae species (Watanabe and Ackman 1974). Thus phospholipid composition data for the same species obtained by different investigators should be comparable even though the area of collection and the time of the year may be different. For example, the phospholipid data for *Euphausia pacifica* from British Columbia (Table 2) are comparable with similar data for *E. pacifica* from California (Van der Veen et al. 1971). The phospholipid composition of *Pasiphaea pacifica* and *Conchoecia elegans* from Bute Inlet (Table 2) were close in composition to these same species collected later in the year in more southern inlets (J. Sargent unpublished data; R. F. Lee unpublished data). Temperature might be expected to effect phospholipid unsaturation in species which occur over a wide range of temperature (Morris 1971).

In contrast to the phospholipids, the neutral storage lipids, namely wax esters and triglycerides, are assumed to be a reflection of both de novo synthesis and dietary fatty acids. Thus the polyunsaturated C_{16} and C_{18} acids which are important components of phytoplankton (Ackman et al. 1968; Chuecas and Riley 1969; Harrington et al. 1970; Kates and Volcani 1966; Patton et al. 1966) were absent or in trace amounts in the zooplankton phospholipids and abundant in the neutral lipids of zooplankton assumed to be at least partly herbivorous, namely the copepods, *Calanus plumchrus* and *Eucalanus bungii*, and the juvenile euphausiid, *Euphausia pacifica* (Nemoto 1968, 1970). In other, presumably carnivorous zooplankton, these polyunsaturated C_{16} and C_{18} acids were minor components, except in *Beroe cucumis* where 16:3 acid was 7 and 9% in the wax esters and triglycerides, respectively. Lebour (1922, 1923) found algae and crustacean parts in *B. cucumis* but other workers indicate that this food could have come from the primary food of *Beroe* which is other species of ctenophore (Swanberg 1974 and references cited therein). In the arctic copepod, *Calanus hyperboreus*, the polyunsaturated C_{16} and C_{18} acids were found only in the summer when phytoplankton were most abundant. These acids were absent or in trace amounts during the other seasons (Lee 1974). Most of our Bute Inlet samples were collected in the spring when phytoplankton levels were high.

The principal alcohols, 20:1 and 22:1, are assumed to arise by de novo synthesis as the corresponding fatty acids, which are the alcohol precursors, are minor components of marine phytoplankton (see reference above). The 20:1 and 22:1 are the principal alcohols of many upper water zooplankton (Table 2; Ackman et al. 1974; Lee et al. 1972; Patton et al. 1972) and the role of these long chain monethylene alcohols for buoyancy has recently been discussed by Ackman et al. (1974). Deeper water zooplankton generally have 16:0 as the principal alcohol (Lee et al. 1971; Morris 1972). The arctic copepod, *C. hyperboreus*, from deep water had wax esters with 16:0 alcohol as a major component whereas those from upper waters had principally 20:1 and 22:1 alcohols (Lee 1974). We cannot offer a satisfactory explanation why one group of zooplankton synthesize primarily 20:1 and 22:1 alcohols and a second group synthesizes mainly 16:0 alcohol.

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Mouth and Mode of Feeding of Caligidae (Copepoda), Parasites of Fishes, as Determined by Light and Scanning Electron Microscopy

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KABATA, Z. 1974. Mouth and mode of feeding of Caligidae (Copepoda), parasites of fishes, as determined by light and scanning electron microscopy. J. Fish. Res. Board Can. 31: 1583–1588.

The structure of the caligid mouth tube is examined by light and scanning electron microscopy in examples of *Caligus curtus*, *C. clemensi*, and *Lepeophtheirus salmonis*. Special attention is directed to the intrinsic musculature of the labrum. A new masticatory apparatus is described, consisting of a divided dentiferous bar at the tip of the labium and referred to as a *strigil*.

A new concept of the mode of feeding is presented. The tissues of the fish are scraped off by movements of the *strigil* and the debris is then picked up by the mandibles which initiate its passage into the buccal cavity. Its transport is assisted by contractions of labral musculature, capable of creating a propelling, peristaltic wave.

KABATA, Z. 1974. Mouth and mode of feeding of Caligidae (Copepoda), parasites of fishes, as determined by light and scanning electron microscopy. J. Fish. Res. Board Can. 31: 1583–1588.

L'auteur examine, par microscopie photonique et électronique à balayage, la structure de la bouche des caligidés sur des exemplaires de *Caligus curtus*, *C. clemensi* et *Lepeophtheirus salmonis*. Il porte une attention spéciale à la musculature intrinsèque du labrum. Il décrit un appareil masticateur nouveau, consistant en une barre dentifère divisée, située à l'extrémité du labrum, qu'il désigne sous le nom de *strigile*.

Il présente un concept nouveau du mode d'alimentation. Les tissus du poisson sont râclés par des mouvements du *strigile*, et les débris sont ensuite saisis par les mandibules qui amorcent leur passage dans la cavité buccale. Le transport des débris est facilité par des contractions des muscles du labrum, capables de créer une onde péristaltique propulsive.

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PARASITIC copepods inflict mechanical damage on their fish hosts either during the course of attachment or by feeding, often by both. As regards copepods belonging to the family Caligidae, Kabata and Hewitt (1971) concluded that the attachment of the caligids and their movements over the surface of fishes contribute little or nothing to the obvious damage resulting from their activities. In the view of these authors, feeding of the copepods was mainly, or even solely, responsible for the damage caused.

Knowledge of the feeding mechanisms and processes of fish parasites has always been of interest to those concerned with the welfare of the fish. In spite of that interest we still know very little about them, particularly where copepod parasites are concerned. This inadequate knowledge is largely due to our inability to observe directly the mouth parts of these parasites in action. Until technological progress provides us with some means of conducting such observations, almost all that we can do is to study the structure of the mouth and buccal appendages and try to infer from that structure the probable mode of action. The process must be regarded as somewhat conjectural, though a skilled observer can be reasonably successful and accurate in his interpretations.

The most recent detailed description of the mouth tube of a caligid copepod, *Caligus curtus* Müller 1785, accompanied by such an interpretation, was published by Parker et al. (1968). In their concept

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of the working of the mouth parts these authors ascribed the dominating role to the mandibles as the main food-gathering appendages. They pointed out the presence of the intralabral muscles and their part in enlarging the buccal cavity, with the resultant drop in intrabuccal pressure. They also observed the presence of "transversely flat ingrowths or horns" in the proximal, lateral corners of the mouth and suggested that they are involved in closing off the oesophageal valve.

The advent of the scanning electron microscope extended our abilities to observe structural details and provided us with new evidence that can be used in interpreting the functional morphology of the mouth parts. This paper is intended to take another look at the structure of the mouth tube of the caligid copepods and to form a new concept of the mode of feeding of these copepods in the light of that new evidence.

Materials and Methods

The structure of the mouth tube was studied from serial sections of *Caligus curtus*, cut at 10 μ and stained with haematoxylin–eosin. Electron microscope studies were carried out on specimens of *C. curtus*, *Caligus clemensi* Parker and Margolis 1964 and *Lepeophtheirus salmonis* (Krøyer 1838). Specimens of all three species were fixed in formalin, dried in Bomar-900 critical point drying apparatus (with Genesolv-D as intermediate and Freon-13 as transition fluid), coated with gold, and studied with ETEC Autoscan B-1 microscope.

Structure of Mouth Tube

The general appearance of the mouth tube of *C. curtus*, representative of the majority of the caligid copepods, was adequately described by Parker et al. (1968). Figure 1, a modification of Fig. 54 of these authors, is shown here to refresh the readers'

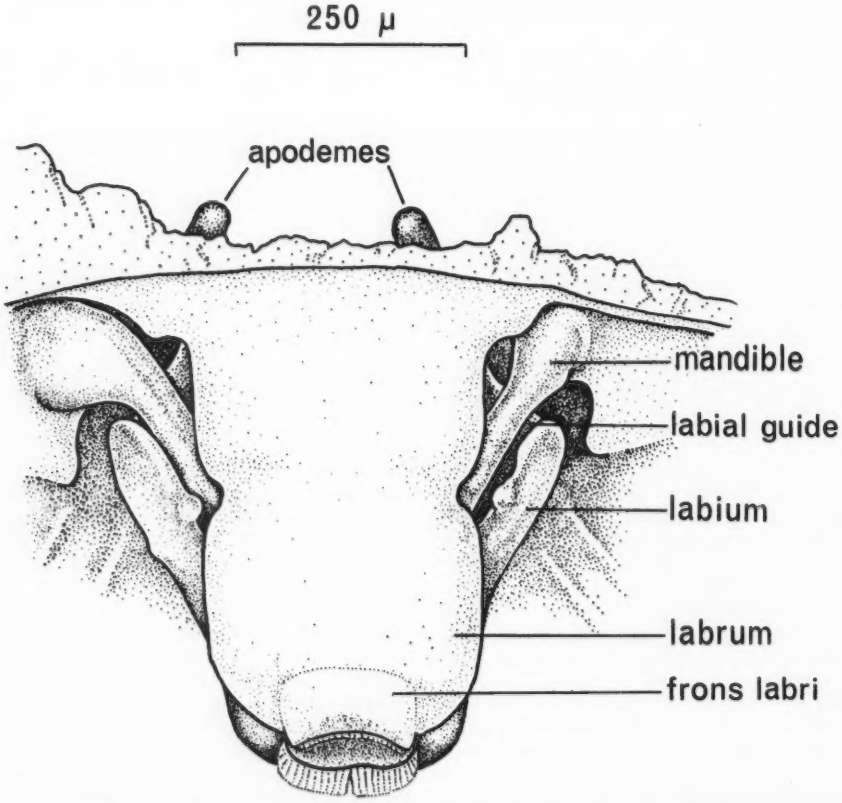


FIG. 1. *Caligus curtus*, mouth, general view (modified from Parker et al. 1968).

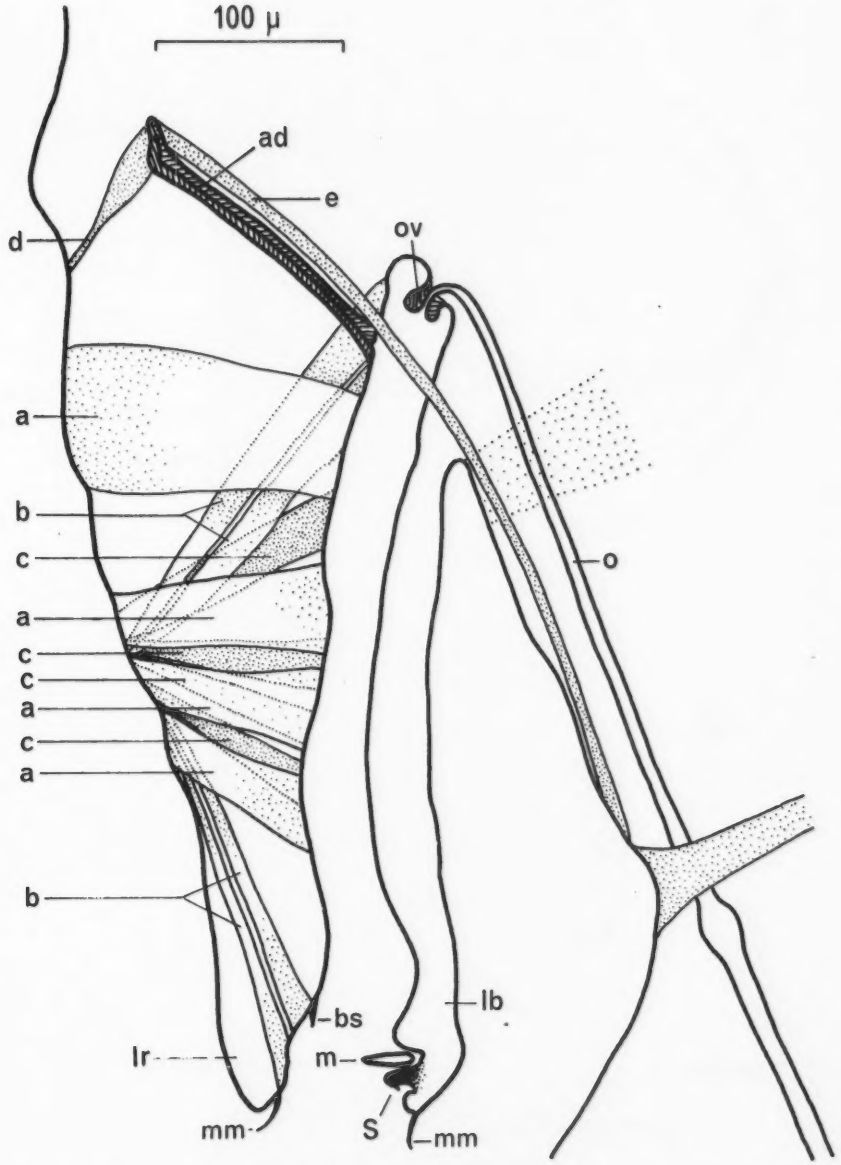
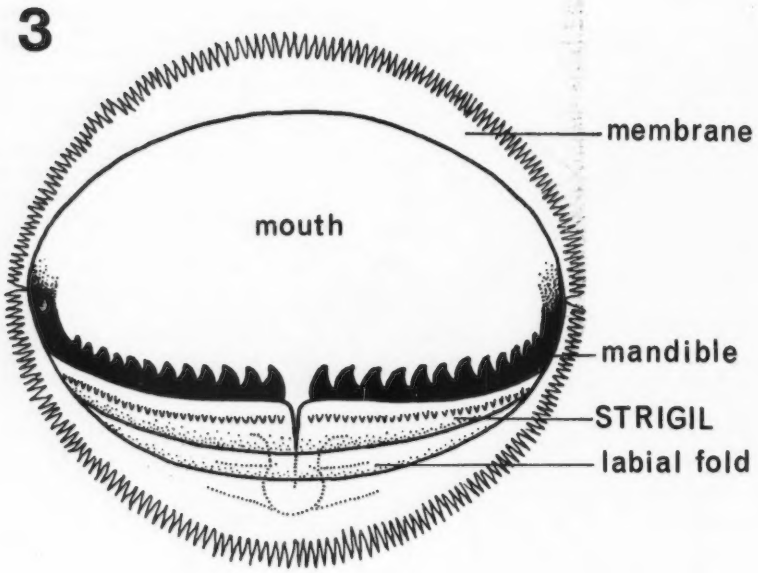
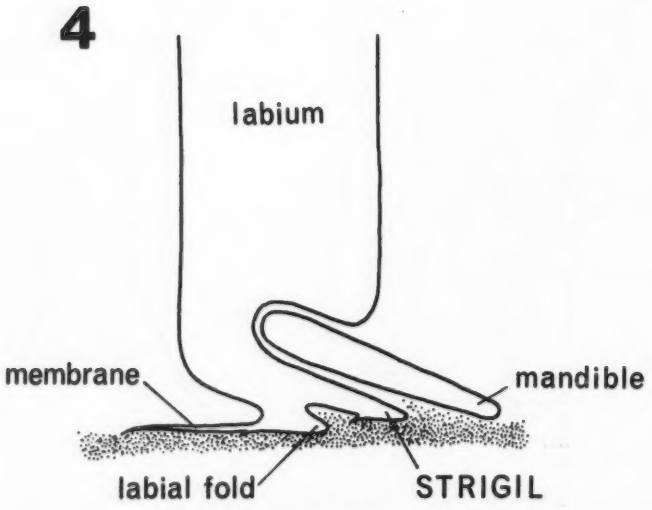


FIG. 2. *Caligus curtus*, mouth tube, sagittal section (diagrammatic). a, *compressores labri laterales*; ad, apodeme; b, *contractores labri*; bs, buccal stylets; c, *compressores labri mediales*; d, *depressor labri*; e, *levator labri*; lb, labium; lr, labrum; m, mandible; mm, marginal membrane; o, oesophagus; ov, oesophageal valve; S, *strigil*.





FIGURES 3–4

FIG. 3. Face-on view of buccal orifice (diagrammatic); FIG. 4. Sagittal section through tip of labium (diagrammatic).

PLATE I. Tip of labium, detail. A, *Caligus clemensi*, ×2000; B, *Caligus curtus*, × 800; C, *Lepeophtheirus salmonis*, × 676.

memory and to bring to attention two structural points not sufficiently stressed in that publication. The first point relates to the two "ingrowths or horns" projecting from the proximal ends of the buccal capsule. Partly exposed by dissection, these are the "endoskeletal" apodemes, functionally very important. The second point is the existence of a small area on the tip of the labrum, referred to as *frons labri*. (Most authors, Parker et al. [1968] included, refer to the two lips of the caligid mouth as upper and lower or ventral and dorsal. These designations are correct, however, only for one of many possible positions of the tube and can be misleading. I have decided, therefore, to revert to the names *labrum* and *labium*, in full awareness that they are not necessarily homologous with these structures in other arthropods.) The reader is requested to note the position of the mandibles, their entry into the mouth tube, and their association with the labial guides, described in detail by Parker et al. (1968).

The musculature of the labrum has not been described previously. A semi-diagrammatic representation is shown in Fig. 2. The apodemes (ad, Fig. 2), arising as invaginations from the lateral, proximal corners of the buccal cavity, are equipped with a pair of antagonistic muscles. *Levator oris* (e, Fig. 2) consists of two long, thin bands of muscle (one only shown in Fig. 2) running from the tip of the apodeme across the base of the mouth tube and for some distance along the ventral surface of the body. A short muscle, *depressor oris* (d, Fig. 2) connects the tip of the apodeme with the wall of the labrum near its base.

The labrum is much thicker than the labium and is very muscular. No muscles have been found in the labium. There are three groups of muscles in each half of the labrum. The outermost group of four muscles (a, Fig. 2) are *compressores labri laterales*. The muscles of this group vary in width, the one closest to the base of the labrum being the broadest, the remaining three measuring about a half of its width. The innermost group, also consisting of four muscles (c, Fig. 2), are *compressores labri mediales*. The muscles of this group are less powerful than those of the *laterales* group. They all originate close together near the midlength of the labrum on its outer wall and diverge along their courses towards the inner wall, so that their insertions on that wall are at about the same level as those of the *laterales* group. Between the two groups are *contractores labri* (b, Fig. 2), comprising two pairs of long, slender muscle bands. *Contractor labri inferior* originates near midlength of the labrum on its outer wall and inserts near the tip of its inner wall; *contractor labri superior* has its origin slightly proximal to that of the other pair and inserts at the base of the labrum, on its inner wall, in the vicinity of the apodeme. Near the insertion of the *contractores labri inferiores* the inner wall of the labrum bears a pair of simple buccal stylets (bs, Fig. 2). These structures, well known in the lernaeocerids (Kabata 1962; Gooding and Humes 1963), have not been previously reported in Caligidae.

The thin labium is intimately associated with the mandibles (m, Fig. 2), appendages closely confined for a part of their length in the labial guides (Fig. 1). Following the curving outline of the tip of the labium, the course of the guides is also curving, as are the tips of the mandibles themselves. The tip of the labium represents the most important part of the mouth tube. It is shown in Fig. 2 but an enlarged diagrammatic representation of its sagittal section is shown in Fig. 4. Figure 3 is a face-on view of the buccal orifice, greatly simplified (there is no indication of the separation between the two lips). The rim of both lips is fringed by a marginal membrane (mm, Fig. 2). Close to it, the surface of the labium carries a ridge, the labial fold (Fig. 4). Proximal to the fold is a hard cuticular bar, referred to here as the *strigil*. The bar consists of two curving halves meeting in the middle and joining in a common cuticular swelling at the base, embedded in the tissues of the labium and detectable in sections only (Fig. 3). The most important feature of the *strigil* is the presence of fine, sharp teeth on its outer wall, close to the base. Each half carries about 50 such teeth. Plate I shows the details of the *strigil* in the three species of caligids investigated. The teeth of the *strigil* are not uniform, increasing slightly in size towards their lateral ends, slightly overlapping and pointing inwards (especially in Plate I, A). The inner wall of the *strigil* provides the outer wall for the labial guide, containing the mandible, with its teeth pointing towards the lumen of the buccal cavity (Plate I, B, C). In Plate I, C the right mandible has been dislodged from the guide during dissection to remove the tip of the labrum. The floor of the mouth behind the labial guide tends to become depressed, forming a shallow cavity running for some distance into the mouth (Fig. 2 and Plate I, B, C).

Mode of Feeding

While moving over the surface of the fish, caligid copepods hold their mouth tubes folded along the ventral surface of the body, their buccal orifices pointing backwards. This fact can be observed with the aid of an inverted microscope. All that follows is speculation based on morphological evidence.

To feed, the copepod must place the tube in a position perpendicular to its body. This could be effected by contractions of the *levatores oris* (e, Fig. 2), the force of which is transmitted to the tube through the apodemes (ad, Fig. 2) acting as levers. In that position the mouth can be applied to the surface of the fish. The marginal membrane spreads around it and seals it from the outside. The membrane, striated and greatly frayed, is equipped in some species (e.g. *Caligus curtus*, Plate I, B) with a row of short setae along the base, further increasing its insulating properties. A slight drop in intrabuccal pressure is needed to maintain firm contact between the mouth and the skin of the fish. It could be produced by contraction of all or some of the 16 muscles in *compressores labri* groups. (The tip of the mouth tube could also be pushed into the skin by some mechanisms extrinsic to the mouth itself, e.g. by depression of the central part of the dorsal shield.) Whatever the mechanism, pressing of the mouth into the skin would push away the labial fold and expose to the skin the divided bar of the *strigil*, bringing its teeth into contact with the fish tissues (Fig. 3 and 4). A rythmic fluctuation in the pressure pushing the tip of the labium into the skin would cause the two halves of the *strigil* to move away from each other, pivoting on the common base, each divergent move being followed by a convergent one. As can be supposed from their structure (Plate I, B), the teeth of the *strigil* would execute sawing movements, particularly effective during their inward stroke. The tissues of the fish would be subjected to the ravages of about 100 fine and sharp teeth, with the resulting accumulation of tissue debris. The debris can then be picked up from the surface by the movements of the mandibles, the mandibular teeth acting as conveyors moving the fish tissue into the buccal cavity.

Some change in the position of the mouth might be necessary for the mandibles to come in contact with the debris produced by the action of the *strigil*. Such change could be produced by a combined and complicated action of the musculature. *Contractores labri*, acting in unison, can lift slightly the *frons labri* and break the seal, allowing the mouth to move. *Depressor* and *levator oris* would act ointly to control the backward slide of the mouth tube, while the *contractores labri* would maintain sufficient pressure within the buccal cavity to prevent a complete loss of contact between it and the surface of the host. A sequential contraction of *contractores labri* would be capable of producing a peristaltic pressure wave further propelling the particles of the fish tissue into the buccal cavity. Some mechanism of this kind is required, because the movements of the mandibles themselves can convey these particles only near the tip of the mouth. The movements must be limited by the length of the mandible and by lack of sufficient flexibility of their bases, not capable of withdrawing for distances that would allow the mandibular teeth to traverse the entire length of the mouth tube.

When feeding is completed, the mouth tube can be folded again by relaxation of the *levator oris* and contraction of the *depressor oris*.

While the above mode of action has not been observed in vivo, it can be postulated with some justification from the morphological evidence. For example, the divergent movements of the *strigil* is supported by the fact that the tissue between the two halves is often loose and folded (Plate I, B, C). The mandibular teeth, seen at close quarters (Plate I, B) do not impress one as capable of effective mastication. No such doubts can be inspired by the appearance of the teeth found on the *strigil*. The important conclusion of these observations is the relegation of the mandibles from the role of the main food gathering appendages, with the consequent change in the concept of the mode of feeding.

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Atheresthes stomias (Jordan and Gilbert 1880) (Pisces: Pleuronectiformes) and its Eye Parasite *Phrixocephalus cincinnatus* Wilson 1908 (Copepoda: Lernaeoceridae) in Canadian Pacific Waters

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KABATA, Z., AND C. R. FORRESTER. 1974. *Atheresthes stomias* (Jordan and Gilbert 1880) (Pisces: Pleuronectiformes) and its eye parasite *Phrixocephalus cincinnatus* Wilson 1908 (Copepoda: Lernaeoceridae) in Canadian Pacific waters. J. Fish. Res. Board Can. 31: 1589–1595.

Based on the examination of more than 3000 fish, the length and age structure of a population of *Atheresthes stomias* are described. In offshore waters the modal length for the males was 36–40 cm, that for the females 41–45 cm. In inshore waters smaller fish predominated. The modal age for the males was estimated to be 5 yr, that for the females 7 yr. The shallow water population was younger. With increase in depth of habitat, both age and length of the fish increased, but abundance decreased.

Atheresthes stomias feeds on a varied diet, dominated by crustacean species but abounding also in fish, including its own species.

Infection with *Phrixocephalus cincinnatus* diminished with the length and the age of the host, as well as with depth of habitat. The number of fish that appear to have withstood monocular infection with *P. cincinnatus* was small. Binocular infection seemed to be almost invariably fatal.

KABATA, Z., AND C. R. FORRESTER. 1974. *Atheresthes stomias* (Jordan and Gilbert 1880) (Pisces: Pleuronectiformes) and its eye parasite *Phrixocephalus cincinnatus* Wilson 1908 (Copepoda: Lernaeoceridae) in Canadian Pacific waters. J. Fish. Res. Board Can. 31: 1589–1595.

Les auteurs décrivent la structure en longueur et en âge d'une population d'*Atheresthes stomias*, fondée sur l'examen de plus de 3000 poissons. Dans les eaux du large, la longueur modale des mâles est de 36–40 cm, celle des femelles 41–45 cm. Dans les eaux côtières, les poissons plus petits prédominent. On a estimé à 5 ans l'âge modal des mâles, et à 7 ans celui des femelles. La population des eaux peu profondes est plus jeune. L'âge et la longueur des poissons augmentent tous deux avec la profondeur, mais l'abondance diminue.

Atheresthes stomias a un régime alimentaire varié, avec prédominance d'espèces de crustacés, mais abondant également en poissons, y compris sa propre espèce.

L'infestation par *Phrixocephalus cincinnatus* diminue avec la longueur et l'âge de l'hôte, de même que la profondeur de l'habitat. Le nombre de poissons qui semblent avoir résisté à l'infestation monoculaire par *P. cincinnatus* est petit. Une infestation binoculaire semble presque invariablement fatale.

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Atheresthes stomias (Jordan and Gilbert 1880) is a member of the family Pleuronectidae ranging in distribution from Central California to the Bering Sea (Hart 1973). Known under the common name of turbot, arrowtooth flounder or longjaw flounder, this elongate and slender fish is distinguished by its drab, brown coloration and the long gape of its mouth, studded with needle-pointed, barbed teeth. It looks, and is, a predatory animal.

Atheresthes stomias has been fished, at times extensively, for use as animal (mink) food and as such has been the dominant item in landings for that purpose on Canada's Pacific coast (Forrester 1968). It has also been fished for these purposes along the coasts of Washington and Oregon and in recent years has had acceptance in fillet form for human consumption. Exploitation has been with

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trawl nets fished at depths ranging from 18 to 183m (10–100 fath).

One of the striking features about this fish is the frequency of infection of its eyes with a large and easily noticeable parasite, a lernaeoceran copepod *Phrixocephalus cincinnatus* Wilson 1908, which has been the object of a special study (Kabata 1967, 1969). Examination of infected eyes suggested strongly that the final outcome of the copepod's presence was blindness. For a predatory fish infection of both eyes is likely to end in death by starvation. It is seldom that a single parasite species exerts such a decisive influence over its host, an influence probably far outweighing that of any other parasite that might be simultaneously present. Consequently, the *A. stomias-P. cincinnatus* system appeared to offer possibilities for studying interactions involving two species, with few complicating factors.

The promise was not altogether fulfilled. As the information on the parasite was being collected, however, notes were being kept also on the host fish. In view of the general dearth of data on *A. stomias*, it was deemed worthwhile to report on the outcome of this collection. This paper contains information on the host, as well as on the patterns of distribution of the parasite in the host population. Since the sampling was not primarily designed for the study of the fish, the data reported on below are not to be considered in the same light as those obtained by regular ichthyological investigations which for *A. stomias* are unfortunately rare.

Materials and Methods

In the course of the fisheries biology cruise of the research vessel *G. B. Reed* in May–June 1968 (Harling et al. 1968) to grounds off the west coast of Vancouver Island, samples of *A. stomias*, taken by trawl, were measured, sexed, and examined for the presence of the copepod. At that time only the adult parasite could be taken into account, since the preadult part of its life cycle was not yet known. Whenever possible all turbot caught were examined. When the catch was large, a random sample was taken. Otoliths were removed for later age determination and stomachs were preserved in formalin. In all, 1397 fish were measured (total length), sexed, and had their otoliths removed.

To obtain information on *A. stomias* in shallow water, sampling was carried out in August 1968 at the entrance to Barkley Sound, using the research vessel *Investigator No. 1*. During the course of this sampling the preadult stages of the parasite were discovered and reported on subsequently (Kabata 1969). As it was determined that there was no correlation between the sex of the host and infection with the copepod, sexing of the fish samples was abandoned.

Another cruise of the *G. B. Reed* was made in May 1969, *A. stomias* being sampled and examined from catches along the west and north coasts of Vancouver Island. The total number of fish sampled during all cruises was 3607. During the 1969 cruise all fish had their eyes carefully examined, each eyeball being opened and scrutinized as soon as possible after capture of the fish.

Records kept following the discovery of the preadult stages discriminated between the fully metamorphosed, externally protruding adult and the less modified juvenile still contained within the eye. Also taken into account were "old injuries," i.e. traces of parasitization evident in the destruction of the eye, decrease in size or partial damage of the lens, and the presence of *P. cincinnatus* remains.

Structure and Distribution of the Population of *A. stomias*

The length distribution of the fish taken on offshore grounds in the May–June cruise in 1968 (both infected and uninfected) is shown in Fig. 1A. There is a considerable difference between length composition of males and females. The length range of the males was much narrower and its upper limit did not extend beyond 60 cm. Not more than 10% of males measured were larger than 45 cm and the largest proportion (just over 70%) was in the 36–40-cm group. The range of female lengths was much greater and extended to 80 cm or close to the maximum recorded length of 84 cm (Hart 1973). In the shallow waters of the entrance to Barkley Sound the fish (sexes combined) were smaller (Fig. 1B). Only 9% of fish sampled in that locality were over 45 cm long, 41% being in the 26–30-cm length-group.

The estimated age structure of the fish sampled (as determined from otolith reading) is shown in Fig. 2A and is similar in pattern to that of length frequency distribution. Dominant ages in males were 5 and 6 yr (35.1 and 30.9%, respectively), in females 6–8 yr (56.5% of female fish sampled). Greatest age determined for males was 10 yr and for females 20 yr. There appeared to be a similar growth rate for both sexes to about 8 yr of age (Fig. 2B). The age composition of smaller fish sampled in Barkely Sound (sexes combined) was, not unexpectedly, much younger than those offshore. The predominant age was 3 and the oldest fish was 12 yr of age (Fig. 2A).

Abundance of *A. stomias* sampled in the region of 48°30′N 124°40′W varied with depth and there was a marked decrease in abundance at depths greater than 420 m (230 fath) (Table 1), a situation similar to that observed for British Columbia waters by Alverson et al. (1964). Length composition of fish sampled also varied with depth. Both male and female fish tended to be smaller at shallower depths (128–164 m [70–90 fath]). Increase in length

with depth was most marked for females. The modal length of all females examined from offshore grounds in 1968 was 41–45 cm. At 128–164 m (70–90 fath) 36.7% of the females were less than 41–45 cm long. At 166–274 m (91–150 fath) the proportion dropped to 31.3%, at 276–366 m (151–200 fath) to 27.2%, and at more than 366 m (200 fath) to 8.1%. There was a corresponding change in estimated age with depth. At 128–164 m (70–90 fath) 48.0% of females were younger than 7 yr and 26.0% older. At depths over 366 m (200 fath) these figures were 8.0 and 83.0%, respectively. Similarly, in males at 128–164 m (70–90 fath) 35.0% were younger than age 5 and the proportion declined steadily until at depths of over 366 m (200 fath) it was only 3.0%.

Diet of *A. stomias*

Stomachs of 753 *A. stomias* were examined for contents in 1968 and 1969. Approximately 70% contained no food and contents of the remainder were identified in most instances. Food items observed were as listed below. Each item is followed by a number in parentheses, representing number of finds.

Crustacea

Thysanoessa spinifera (183)

Euphausia pacifica (109)

Unidentified euphausiid remains (47)

Pandalus montagui tridens (41)

Pandalus jordanii (37)

Pandalus sp. (28)

Crangon communis (2)

Crangon alaskensis (1)

Crangon sp. (1)

Unidentified shrimp remains (1)

Mollusca

Gonatus magister (2)

Unidentified cephalobod remains (1)

Echinodermata

Strongylocentrotus sp. (1)

Pisces

Thaleichthys pacificus (Osmeridae) (32)

Clupea pallasii (Clupeidae) (15)

Ammodytes hexapterus (Ammodytidae) (13)

Atheresthes stomias (Pleuronectidae) (1)

Lepidopsetta bilineata (Pleuronectidae) (3)

Lyopsetta exilis (Pleuronectidae) (6)

Parophrys vetulus (Pleuronectidae) (2)

Citharichthys sp. (Bothidae) (1)

Theragra chalcogramma (Gadidae) (1)

Anoplopoma fimbria (Anoplomatidae) (6)

Agonus acipenserinus (Agonidae) (2)

Cymatogaster aggregata (Embiotocidae) (1)

Engraulis mordax (Engraulidae) (2)

Lumpenella longirostris (Stichaeidae) (1)

Annelida

Unidentified polychaete remains (2)

Merluccius productus (Merlucciidae) (2)

Sebastes alutus (Scorpaenidae (1)

Sebastes sp. (1)

Unidentified flatfish remains (2)

Unidentified gadid remains (3)

Unidentified fish remains (34)

By far the most common food taken by turbot were Crustacea (451 finds), followed by fish (132 finds). Among the former the pelagic euphausiids predominated (339 finds). Similar tendency could be seen among the fish taken. The most commonly found species were *Thaleichthys pacificus* and *Clupea pallasii* (47 finds in all), both with the off-the-bottom mode of life. The inclusion of many definitely benthic species, both vertebrate and invertebrate, suggests that *A. stomias* feeds in a variety of habitats, though it appears to forage most commonly in midwater.

There were no differences in the qualitative composition of the food content of infected and uninfected fish (though only infected fish with monocular infection could be used for comparison with healthy fish). Out of 262 stomachs examined in 1969, 11.2% of the infected and 10.8% of the uninfected fish contained vertebrates only; 73.3% of the infected and 76.3% of the uninfected fish contained invertebrates only, and 15.5% of the infected and 12.8% of the uninfected contained both.

Distribution of *Phrixocephalus cincinnatus* in Host Population

Even a cursory examination shows that *P. cincinnatus* does not occur with uniform frequency throughout its host population. The differences in infection with size of the host are shown in Table 2.

It is clear that the smallest length-groups are particularly heavily attacked, the level of infection generally dropping with the increase in length of the fish. The decrease is not so pronounced in the fish of the shallow waters in the entrance to Barkley Sound, but a gradual decrease with length is also manifest there. Of interest also is the fact that the infection levels of the Carmanah fish are generally lower than those found in the inshore fish.

As can be expected, the differences in infection with the estimated age of the host were roughly parallel to those shown by the differences with its length. The fish of young age (and, therefore, probably of smaller length) were more heavily parasitized than those of the older age-groups.

It seems, in view of the above, that the depth of habitat may play some part in determining the level

of parasitization. Table 3 shows data dealing with the differences in parasitization with depth.

The data for the depth less than 91 m (50 fath) are from the Barkley Sound area, the remainder from the Carmanah grounds. It can be seen that the proportion of the host population infected decreases by about 9 times with the doubling in the depth of the habitat. In number of parasites per fish it drops by about 17 times, whereas in number per infected fish it is about halved. It must be remembered, of course, that the overall reduction in infection is also influenced by the composition of the host population. The deeper dwelling fish are generally longer and older and such fish are apparently less prone to attack by *P. cincinnatus*.

The parasite population, then, gradually decreases in numbers with increasing length and age of the host and depth of its habitat. The age of the parasite population is also affected. The total number of parasites discovered during the May 1969 cruise was as follows:

Adults	88
Juveniles	621
Injuries (monocular)..	89
Injuries (binocular) ..	2

The disproportion between the number of adult and juvenile parasites is particularly striking. It suggests that many parasites do not reach the adult stage, even though they succeed in infecting the definitive host. Below the depth of 70–90 fath no adults were found, only juvenile stages being present within the eyeballs of fewer and larger fish (Table 3). Fish of 16–20-cm length-group carried only the adults of *P. cincinnatus*; fish longer than 26–30 cm never had more than 20% of adults in the parasites they carried. Juveniles only were present in fish longer than 61–65 cm.

Equally striking are the changes in the occurrence of binocular infection. Table 3 shows that, whereas in waters less than 91 m (50 fath) deep this infection occurs in about 10% of fish, it is virtually absent from the offshore, longer and older fish. None was found in water deeper than 164 m (90 fath).

The figures on the "old injuries," representing fish which have survived the attack of *P. cincinnatus*, are also interesting. In the inshore waters, where more than 50% of *A. stomias* are infected, not more than 1.5% of the fish examined were found with one eye damaged by the parasite. The number for both eyes damaged was only 0.1% (Table 3). In the offshore waters, at all depths, the proportion

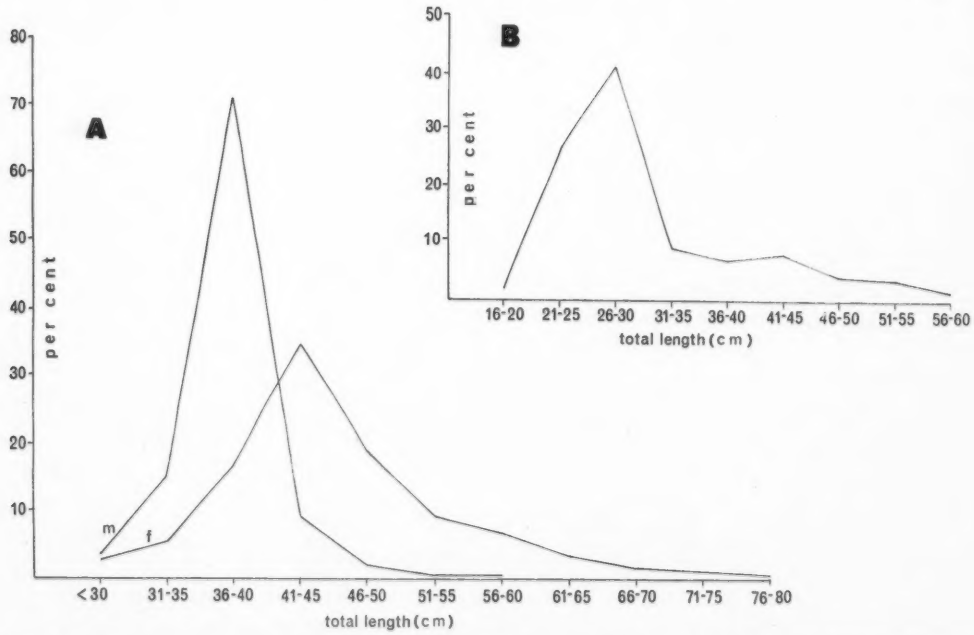

FIG. 1. Length composition of the sample of *Atheresthes stomias* taken in 1968; A, in May–June off the west coast of Vancouver Island; B, in entrance to Barkley Sound, in August. m, males; f, females.

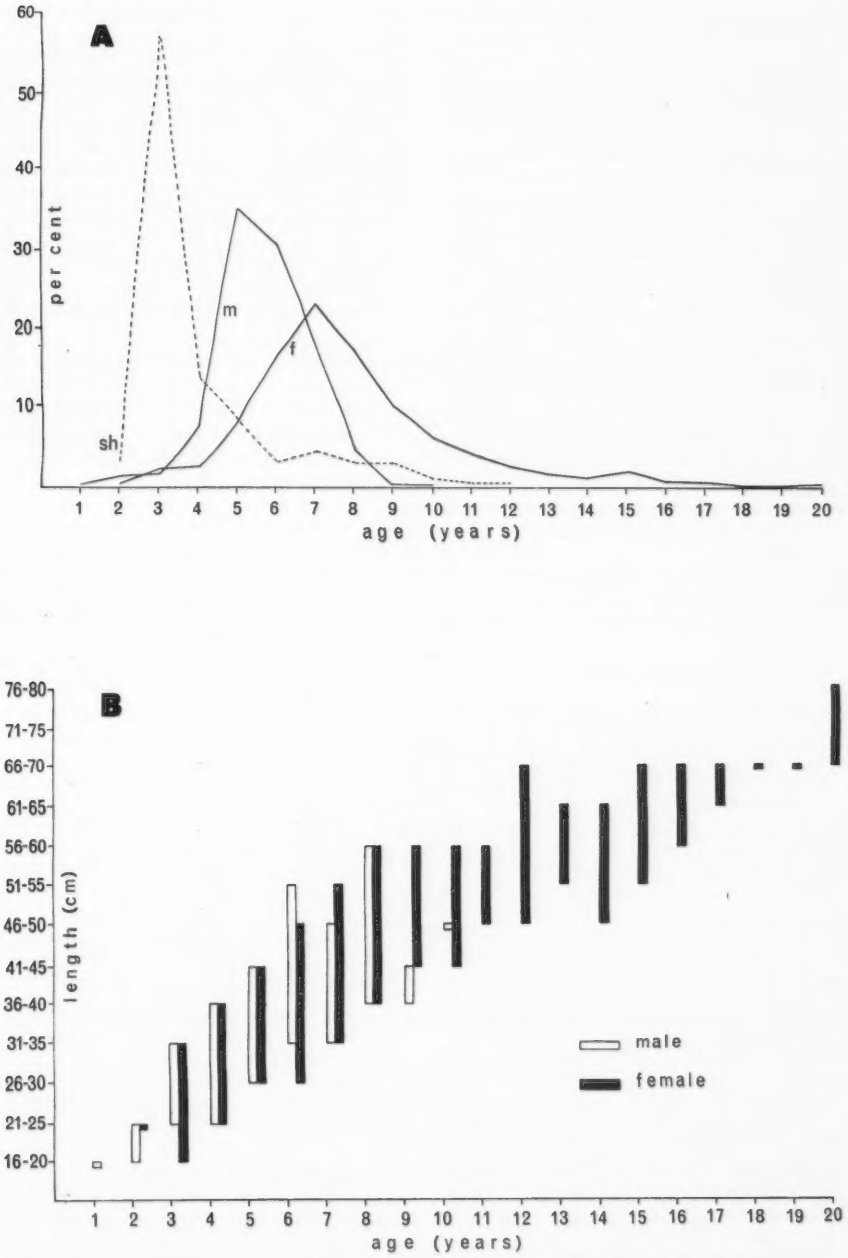

FIG. 2, A, Age composition of the sample of *A. stomias* taken in May–June 1968 in offshore waters and in August 1968 in Barkley Sound; B, Length ranges for *A. stomias* of different ages, combined sample from offshore and shallow waters. f, females; m, males; sh, shallow water fish of both sexes.

of old injuries to one eye was less than 1%. No binocular damage was found.

TABLE 1. Abundance of *Atharesthes stomias* in catches from various depths (fathoms in parentheses).

Depth (*m*)	lb/30 min	Depth (*m*)	lb/30 min
128–135(70–74)	378	342–353(187–193)	253
132–1.5(72–74)	290	380–386(208–211)	278
168–172(92–94)	458	381–382(209–210)	115
203(111)	103	416–420(228–230)	103
234–241(128–132)	545	428(234)	35
274–278(150–152)	130	457–465(254–258)	51
311(170)	205	490–498(268–272)	13
336–351(184–192)	396	513–515(281–282)	33

Discussion

The quantity and character of data accumulated on the population of *A. stomias* are insufficient for authoritative conclusions about it. Some indications, however, are presented about the structure and distribution of the population with depth. It can be presumed that with increasing depth *A. stomias* becomes less abundant and the average age and length increase. With the exception of about 200 fish, all the specimens were caught in May and June. Consequently, nothing can be said about the possibility of seasonal fluctuations in the distribution of the fish. The existence of such fluctuations is

TABLE 2. Incidence of *P. cincinnatus* in *A. stomias* of various length-groups.

Locality and date	Length-group (*cm*)	No. examined	% infected	% binocular infection
Carmanah Ground (entrance to Juan de Fuca Strait, depth 93–183 m [51–100 fath]) May 1969	16–20	4	50.0	–
	21–25	17	35.3	–
	26–30	19	26.3	–
	31–35	81	11.1	–
	36–40	653	16.4	0.61
	41–45	566	14.3	0.17
	46–50	415	19.9	0.96
	51–55	188	13.3	–
	56–60	69	15.9	–
	61–65	18	5.5	5.5
	66–70	17	–	–
	71–75	9	–	–
	76–80	9	11.1	–
	81–85	3	–	–
Barkley Sound (depth 18–37 m [10–20 fath]) Aug. 1968	16–20	2	100.0	–
	21–25	38	92.1	7.9
	26–30	52	90.4	19.2
	31–35	12	75.0	8.3
	36–40	12	66.7	25.0
	41–45	9	66.7	–
	46–50	3	–	–
	51–55	5	40.0	–
	56–60	1	100.0	100.0

TABLE 3. Parasitization of the eyes of *A. stomias* living at different depths with the copepod, *P. cincinnatus*.

	<91 m (*50 fath*)	91–128 m (*50–70 fath*)	128–164 m (*70–90 fath*)	>164 m (*90 fath*)
% infection	58.7	21.5	12.8	6.7
% binocular infection	10.7	0.1	0.5	–
No. parasites/fish	1.81	0.25	0.16	0.09
No. parasites/infected fish	3.1	1.1	1.2	1.4
% fish with old monocular injury	1.5	0.4	0.2	0.7
% fish with old binocular injury	0.1	–	–	–
No. juveniles/adult parasite	7.2	7.1	5.9	no adults

suggested by the data collected during the fishes cruises of *G. B. Reed* (Harling et al. 1968). It is fair to assume, though, that the shallow inshore waters are probably the nursery grounds for *A. stomias* and that the individual fish tend to occupy deeper waters as they grow older.

The course of infection of *P. cincinnatus* and its outcome were discussed in an earlier paper (Kabata 1969). In brief, the parasite enters the eye of the fish while still very small and vermiform. Having moved through the pupillary opening, along the perimeter of the lens, to the bottom of the eye, it pierces the retina and becomes anchored in the chorioid, where it feeds on blood of the fish. With growth, the posterior end of the parasite gradually moves backwards through the eye. The exact mode of penetration of the eye by the abdomen of the parasite is unknown. The iris and the cornea must be penetrated if the parasite is to reach maturity. When the posterior end of the body emerges from the eye, it develops into the trunk containing the reproductive organs and produces voluminous egg sacs.

The early part of the parasite's life history is still unknown. It might or might not involve an intermediate host. At any rate, a fairly brief free-swimming period can be assumed to exist.

In discussing the relationship between *P. cincinnatus* and its host, the possible existence of an intermediate host must be kept in mind. Its existence in the shallow water nears the shore can be instrumental in causing high level of infection in that region. Its absence or scarcity in the deeper water might be partly responsible for the drop in infection level with depth.

The size of the host is likely to have a twofold effect on the parasite. A larger and older fish is a target more easily located by the free-swimming infective stage of the copepod. One would therefore expect that the large size of the fish, other things being equal, should tend to promote infection. The large size of the eye might make its penetration more difficult; it is also probably important on another account. The larger the eye, the longer must be the time required by the young copepod to emerge from it backwards. At some critical size of the eye that period might become too prolonged for the parasite to perform this task and to complete its life cycle. Alternatively, the tissues of the eye might become too solid for the parasite's posterior to push through.

The failure to emerge from the eye means premature death of *P. cincinnatus*. Some of the juveniles recovered from the eyes of large fish were dead and in a state of disintegration. At this stage, probably, the infection ends without causing the total destruction of the eye. Relatively little harm is caused to the host. The decomposition of the larger adult *P. cincinnatus* within the eye, however, seems capable of causing complete destruction of the eye. As suggested by the comparison of the diets of normal and monocular fish, however, the destruction of one eye appears to have no overwhelming effect on the fish, at any rate not immediately. The fish is still capable of capturing its prey. The data available are insufficient to assess whether the general decrease in the infection level with length parallels the decrease in the numbers of fish with old monocular injuries. It is conceivable that the disappearance of the one-eyed fish from the population is selective. (For example, they might be less effective in avoiding predators, or in locating their prey.)

In contrast to the above, the removal of fish with both eyes affected seems to be swift and almost complete. With the exception of two fish found inshore and still quite small, no fish with both eyes affected was found to have survived to display its old injuries.

Another reason for the scarcity of binocular infections is probably found in the morphology of the host's head (Kabata 1969).

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Myxosoma cerebralis: Comparative Sensitivity of Spore Detection Methods

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MARKIW, M. E., AND K. WOLF. 1974. *Myxosoma cerebralis:* comparative sensitivity of spore detection methods. J. Fish. Res. Board Can. 31: 1597–1600.

Physical and biophysical methods of detecting spores of *Myxosoma cerebralis* were used in sequence on 87 individual fingerling rainbow trout (*Salmo gairdneri*) from two populations with a low incidence of infection. Physical methods of releasing spores from the organs of equilibrium, gill arches, or the axial skeleton gave an estimated rate of infection of 2.3–4.6%. Each succeeding step — pepsin digestion, trypsin digestion, and differential centrifugation through 55% dextrose solution — revealed additional infected fish. The final step of the sequence detected 10.5 times more infected fish than were found by examination of the organs of equilibrium or the axial skeleton with physical means; the true incidence was at least 24.1%. Procedures are described for using biophysical methods on 60-fish pools for hatchery inspection work and also on the more bony skeletons of mature fish.

MARKIW, M. E., AND K. WOLF. 1974. *Myxosoma cerebralis:* comparative sensitivity of spore detection methods. J. Fish. Res. Board Can. 31: 1597–1600.

Nous avons utilisé en succession des méthodes physiques et biophysiques pour détecter les spores de *Myxosoma cerebralis* sur 87 alevins individuels de la grosseur du doigt de truite arc-en-ciel (*Salmo gairdneri*) provenant de deux populations à basse fréquence d'infection. Les méthodes physiques de libération des spores des organes d'équilibre, des arcs branchiaux ou du squelette axial donnent un taux d'infection estimé de 2.3–4.6%. Chaque étape successive — digestion à la pepsine, digestion à la trypsine et centrifugation différentielle à travers une solution de dextrose à 55% — découvre encore plus de poissons infectés. L'étape finale de la série révèle 10.5 fois plus de poissons infectés que l'examen des organes d'équilibre ou du squelette axial par des moyens physiques; la fréquence réelle est d'au moins 24.1.% Nous décrivons la marche à suivre pour utiliser les méthodes biophysiques sur des bassins de 60 poissons lors de l'inspection d'établissements de pisciculture, de même que sur les squelettes plus osseux des poissons mûrs.

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To control *Myxosoma cerebralis*, the cause of whirling disease, one must be able to determine whether a population harbors infected individuals. Clinical whirling disease is readily diagnosed and the spore stage, critical to accurate identification, easily recognized. In contrast, subclinical infection, early incubation stages, the carrier state, and low incidences in a population are difficult to detect. Although serological or immunological methods may eventually provide definitive and sensitive detection, only physical, histological, and biophysical methods of detection are now available (MacLean 1971; Prasher et al. 1971; Rydlo 1971; Landolt 1973; Halliday 1973; Markiw and Wolf 1974). Of these, the biophysical methods offer decided advantages because they incorporate digestion to release spores gently for concentration and offer a practical approach to use of pooled samples without risk of loss of sensitivity. The methods vary in the time required for completion of the procedures; they have not been compared for sensitivity, and both factors are important in control programs.

The purpose of our work was to compare several physical methods with biophysical methods for sensitivity of spore detection.

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Materials and Methods

FISH

We used rainbow trout (*Salmo gairdneri*) with low population incidences of *M. cerebralis* infection, but none of the fish showed any clinical signs of whirling

disease. There were four lots of experimentally infected trout — survivors of other research — and one lot of naturally infected trout from a hatchery with a history of whirling disease (Table 1).

Sampling procedure for comparison of physical and biophysical methods

Although they were in four tanks, the 256 fish of Lot I were considered to be a single population. According to calculations given by Ossiander and Wedemeyer (1973), in a population of 250 animals having a disease incidence of 5%, one must sample 49 fish to detect at least one infected individual at the 95% confidence level. We sampled 65 of the 256 trout. All 22 fish of Lot II were individually assayed.

To promote uniformity in testing, one person performed all detection procedures. Four specimens were processed each day, and separate sets of instruments and laboratory ware were used for each fish. After each day's work, instruments and equipment were washed and held in 1:1 (v/v) dilution of household bleach (5.25% sodium hypochlorite) to destroy spores and to prevent their carry-over to the next day's work. A "single blind" approach was used to minimize bias; all specimens were coded and their health or disease status was unknown to the processor.

Stepwise sequence in comparison of physical and biophysical methods

Each fish, in its own container, was killed with anesthesia, measured, weighed, held at 45 C for 3–5 min, and defleshed. The organs of equilibrium and gill arches were removed, the total axial skeleton was weighed, and the material processed in six consecutive steps. A uniform protocol for the spore search was followed throughout the study. Samples of the fluid materials resulting from each of the steps (corresponding with a detection method) were placed in a hemacytometer and both of the ruled areas (1.8 mm^3) were methodically searched at 430× until 5 min had elapsed or spores were found, whichever occurred first. Only typical intact spores having two polar capsules were counted. Occasionally, when only one or two spores were detected in a preparation, identification was confirmed by a second observer.

Table 1. Length, weight, and age of rainbow trout (*Salmo gairdneri*) used.

Lot no.	Length (*cm*)	Wt (g)	Age (*mo*)	Kind of infection
I	6 to 14	4.5 to 36	5	Experimental
II	8 to 14	7 to 32	5	Experimental
III	11 to 14	20 (avg)	13	Natural
IV	10 to 12	25 (avg)	8	Experimental
V	16 to 28	191 (avg)	18	Experimental

Step 1. (Organs of equilibrium method)
Organs of equilibrium were crushed in a mortar, and held in 1 ml of 1% HCl for 20 min.

Step 2. (Gill arches method)
Gill arches were trimmed of filaments, crushed in 2–3 ml H_2O, and allowed to settle 1–2 min.

Step 3. (Axial skeleton method)
Axial skeleton was combined with residues of Step 1 and 2, crushed in 10 ml 0.5% pepsin (w/v) at pH 1.8–1.85 in 0.5% HCl, and allowed to settle 3–5 min.

Step 4. (Pepsin–trypsin–dextrose centrifugation method [Markiw and Wolf 1974])
Residue from Step 3 was brought to 20 ml with pepsin solution and shaken at 37 C for 1–1.5 h. Collected fluid was centrifuged at 1200 × *g* for 10 min at 22 C. The pellet was resuspended in 2 ml water.

Step. 5. Residue from Step 4 was brought to 4 ml and trypsinized. The pellet was resuspended in 2 ml half-strength Hanks' balanced salt solution (BSS), containing 1% bovine albumin fraction V (BSA).

Step 6. Suspended residue from Step 5 was layered onto 1 ml of 55% dextrose in a Shevky-Stafford tube and centrifuged at 1200 × *g* for 30 min at 22 C. The pellet was resuspended in 0.1–0.2 ml half-strength Hanks' BSS with BSA.

Comparison of two biophysical methods

Defleshed axial skeletons from 20 trout from Lot I were pooled, minced, and divided into four 17.5-g samples. Two of the samples were processed with the trypsin method of Landolt (1973) and two with the pepsin–trypsin–dextrose method of Markiw and Wolf (1974). Final residues of each sample were collected in Shevky-Stafford tubes, resuspended in 0.1 ml half-strength BSS, and searched for spores.

Modifications of pepsin-trypsin-dextrose method for large-scale sampling and for use on mature trout

As reported by Markiw and Wolf (1974) about 60% of *M. cerebralis* spores are localized in the head and gills of infected fish. Consequently, only defleshed heads were used in adapting the pepsin–trypsin–dextrose methodology to the kind of population sampling now being done in hatchery inspection work.

Two trials were run in which 60 rainbow trout heads were pooled and processed as a single batch. Processing was carried out according to procedures of Markiw and Wolf (1974) except that, after digestion with trypsin, the material was filtered through a thin layer of glass wool to remove gross particulate matter before concentration and differential centrifugation. Total weight of defleshed and cranial elements was 86 g for 60 Lot IV fish, and 111 g for 60 Lot III fish.

The pepsin–trypsin–dextrose method was also applied to material from two pools of 20 mature fish (Lot V). The only departure from the original de-

scribed procedure was the use of a meat grinder to mince the axial skeletal elements.

Results

Comparison of physical and biophysical methods

Biophysical methods of spore release and concentration revealed more infected fish than did physical methods (Table 2). The pepsin–trypsin–dextrose centrifugation method revealed 21 infected fish among the 87 examined. The biophysical method was 10.5 times more sensitive than the examinations of organs of equilibrium and axial skeleton (each of which revealed two infected fish) and 5.2 times more sensitive than the examination of gill arches (which revealed four infected fish).

The least sensitive physical methods yielded incidences of infection for Lot I and II of 3.1 and 0%, respectively; the most sensitive method (biophysical) gave incidences of 26.2 and 18.1%, respectively.

As stated by Ossiander and Wedemeyer (1973), sample sizes derived in their table were determined for infectious pancreatic necrosis (IPN), and the program could be varied for such factors as population size and disease incidence, and used for other diseases. Accordingly, using the basic program for IPN, the carrier incidences detected by the various methods and also the number of trout in the two populations (278) were inserted and the program was rerun. The analysis showed that at the 95% confidence limits for a population of 278 the numbers of trout that would have to be examined to detect spores by the different methods were as follows: organs of equilibrium or axial skeleton, 94; pepsin digestion, 36; pepsin and trypsin digestion, 18; and enzymatic digestion plus centrifugation through dextrose, 9. The number of trout used in the present study was sufficient to detect spores in the organs of equilibrium or axial skeleton at 90% (but not 95%) confidence limits.

Comparison of trypsinization with pepsin–trypsin–dextrose method

The pepsin–trypsin–dextrose method proved to be more sensitive than the use of trypsin alone. Although a few spores were present in residues from the latter, only a single spore from one sample was found within the ruled grids of a total of eight hemacytometer chambers. In contrast, both samples from the pepsin–trypsin–dextrose method showed spores in the ruled areas of every one of four counting chambers; the averages were 8 and 10.5.

Large-scale sampling and assay of mature specimens

The pepsin–trypsin–dextrose procedures worked effectively in large-scale sampling. A total of 8800 spores was recovered from the 60 experimentally infected trout examined, or an average of 147 spores/head. Although physical methods failed to show spores in the naturally infected fish, the sequential processing released a total of 93,000 spores or an average of 1550/head.

For pooled samples of 60 fish, 6–7 h were required for processing, divided among four steps: 1) decapitation, heating, and defleshing, 1.5 h; 2) pepsin digestion, 3–4 h; 3) trypsin digestion,

Table 2. Comparison of the incidence of *Myxosoma cerebralis* spores detected by physical and biophysical methods.

		Physical methods			Biophysical methods		
Lot no.	Fish no.	Organs of equilibrium	Gill arches	Axial skeleton	Pepsin digestion	Pepsin and trypsin digestions	Pepsin and trypsin digestions + dextrose centrifugation
I	1–15	0	0	0	0	0	0
	16–33	0	1	0	1	1	3
	34–51	2	3	2	4	8	12
	52–65	0	0	0	1	2	2
	Subtotals	2 (3.1%)	4 (6.2%)	2 (3.1%)	6 (9.2%)	11 (16.9%)	17 (26.2%)
II	1–22	0 (0%)	0 (0%)	0 (0%)	0 (0%)	1 (4.5%)	4 (18.1%)
Totals							
No. 87		2	4	2	6	12	21
Percentage		2.3%	4.6%	2.3%	6.9%	13.8%	24.1%

0.5 h; and 4) concentration and centrifugation through dextrose, 1.0 h.

Skeletal elements from mature (Lot V) trout were readily digested. Spore counts were high, averaging 6700/fish in one pool and 10,000/fish in the second pool.

Discussion

Our results indicate that the pepsin–trypsin–dextrose processing sequence is the most sensitive procedure yet developed for detection of spores of whirling disease. Although developed for use on young (fingerling) fish, the method also worked well with mature trout whose skeletons had more bone. Trials in which pools of 60 fish heads from populations with low incidences of *M. cerebralis*, through either natural or experimental infection, showed clearly the suitability of the procedures in practical hatchery inspection work.

Although the total elapsed time required to complete processing 60 fish heads is 6–7 h, the actual working time is about half of that. In hatchery inspection work, the intervening time can be used for bacteriological, parasitological, and virological examinations. As now conducted by federal personnel, the inspection of hatcheries for *M. cerebralis* requires 4–8 h, and much of the time is spent at a microscope (L. L. Pettijohn personal communication). The procedures we describe require less working time and provide a far greater measure of confidence in detection.

Provided that the infection process has progressed to the stage of spore development, the results suggest that the pepsin–trypsin–dextrose method is broadly applicable, as in surveillance, where light infection is sought among mature fish or among fingerlings or fry.

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Fine Structure of the Retinal Pigment Epithelium, Bruch's Membrane, and Choriocapillaris in the Northern Pike (*Esox lucius*)

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BRAEKEVELT, C. R. 1974. Fine structure of the retinal pigment epithelium, Bruch's membrane, and choriocapillaris in the northern pike (*Esox lucius*). J. Fish. Res. Board Can. 31: 1601–1605.

The fine structure of the retinal pigment epithelium, Bruch's membrane, and the choriocapillaris has been studied by light and electron microscopy in the adult northern pike (*Esox lucius*).

The pigment epithelium is composed of a single layer of large cells. Each epithelial cell has abundant mitochondria, smooth endoplasmic reticulum, myeloid bodies, phagosomes, and pigment granules. Rough endoplasmic reticulum and ribosomes are scarce.

The scleral or basal border of the epithelial cell is not infolded whereas the vitreal or apical surface displays numerous, fine, elongated processes which surround the inner and outer segments of the photoreceptors.

Bruch's membrane is composed of three layers. The innermost layer is the basal lamina of the pigment epithelium. The outermost layer is the basal lamina of the choriocapillaris endothelium. Between these basal laminae is a layer of fine fibrils. The overall thickness of Bruch's membrane is 3.5–4 μ posteriorly.

The endothelial wall of the choriocapillaris bordering Bruch's membrane is typically very thin but nonfenestrated. Vesicles are common in the endothelial cytoplasm.

This region of the pike eye differs morphologically from that described for most other vertebrates.

BRAEKEVELT, C. R. 1974. Fine structure of the retinal pigment epithelium, Bruch's membrane, and choriocapillaris in the northern pike (*Esox lucius*). J. Fish. Res. Board Can. 31: 1601–1605.

L'ultra-structure de l'épithélium pigmentaire, la membrane de Bruch et les choriocapillaires ont été étudiés au microscope photonique et électronique chez le grand brochet adulte (*Esox lucius*).

L'épithélium pigmentaire est composé d'une couche unique de grosses cellules. Chaque cellule épithéliale abonde en mitochondries, réticulum endoplasmique lisse, corps myéloïdes, phagosomes et pigments granuleux. Le réticulum endoplasmique hérissé et les ribosomes sont rares.

La bordure sclérale ou basale de la cellule épithéliale n'est pas replié en dedans, alors que la surface vitréale ou apicale montre plusieurs fins procès allongés qui entourent les segments internes et externes des photorécepteurs.

La membrane de Bruch est composée de trois couches. La couche interne est la lamina basale de l'épithélium pigmentaire. La couche externe est la lamina basale de l'endothélium de choriocapillaires. Entre ces laminae basales se trouve une couche de fibrilles délicates. L'épaisseur de la membrane de Bruch est de 3.5–4 μ postérieurement.

La paroi endothéliale des choriocapillaires bordant la membrane de Bruch est typiquement très mince mais non fénestrée. Les vésicules sont communes dans le cytoplasme endothélial.

Cette région de l'oeil du grand brochet diffère morphologiquement de celle déjà décrite chez tous les autres vertébrés.

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THE fine structure of the retinal pigment epithelium, Bruch's membrane, and choriocapillaris has been described in several species (Yamada et al. 1958; Sumita 1961a, 1963; Dowling and Gibbons 1962; Garron 1963; Bairati and Orzalesi 1963; Nakaizumi 1964a, 1964b; Nakaizumi et al. 1964; Breathnach and Wyllie 1966; Leeson and Leeson 1967; Leeson

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1968; Leure-du Pree 1968; Hollenberg and Burt 1969; Braekevelt and Hollenberg 1970; Dickson and Hollenberg 1971).

The notable morphologic features of this region in the vertebrates described, are an attenuated and highly fenestrated choriocapillaris endothelium with many basal infoldings and mitochondria within the epithelial cells. These features are consistent with a rapid diffusion of large amounts of fluid from choriocapillaris to the pigment epithelium. Tracer studies have substantiated this diffusion pathway (Bernstein and Hollenberg 1965a).

As part of a comparative study of the vertebrate retina, the pigment epithelium, Bruch's membrane, and choriocapillaris were studied in the northern pike (*Esox lucius*). The northern pike was chosen as a representative fish having acute vision. It was found that this region, although basically similar to that of other species and presumably also active in metabolic transfer, differs morphologically from that in most other vertebrates.

Materials and Methods

Adult northern pike were collected by netting at various sites in Manitoba and held in large aerated tanks until utilized. For this study one eye from each of 10 animals was examined.

With the fish light-adapted, the eyeball was removed, opened at the equator and fixed for 5 h at 4 C in 5% glutaraldehyde buffered to pH 7.3 with .1 M Sorensen's phosphate buffer. Without detaching the retina, the posterior half of the globe was removed, washed briefly in 5% sucrose in .1 M Sorensen's buffer (pH 7.3), and cut into small pieces with a razor blade. The tissue was post-fixed in 1% OsO_4 in .1 M Sorensen's buffer (pH 7.3) for 2 h at 4 C, dehydrated in ethanol to propylene oxide, and embedded in Araldite.

Pieces of plastic embedded tissue were reoriented using a wax mount. Thin sections were cut on an LKB Ultratome III and mounted on Formvar coated copper grids. Sections were double stained in aqueous uranyl acetate and lead citrate and examined in a Philips EM300.

For light microscopy, thick sections (0.5 μ) were cut, placed on glass slides, and stained with toluidine blue. The sections were examined and photographed with a Wild M20 Photoautomat.

Results

Retinal Pigment Epithelium

The retinal pigment epithelium of the northern pike is composed of a single layer of large cells (Fig. 1) with very long pigment-laden apical processes. These processes which appear to be of only one type extend almost to the external limiting membrane (Fig. 2).

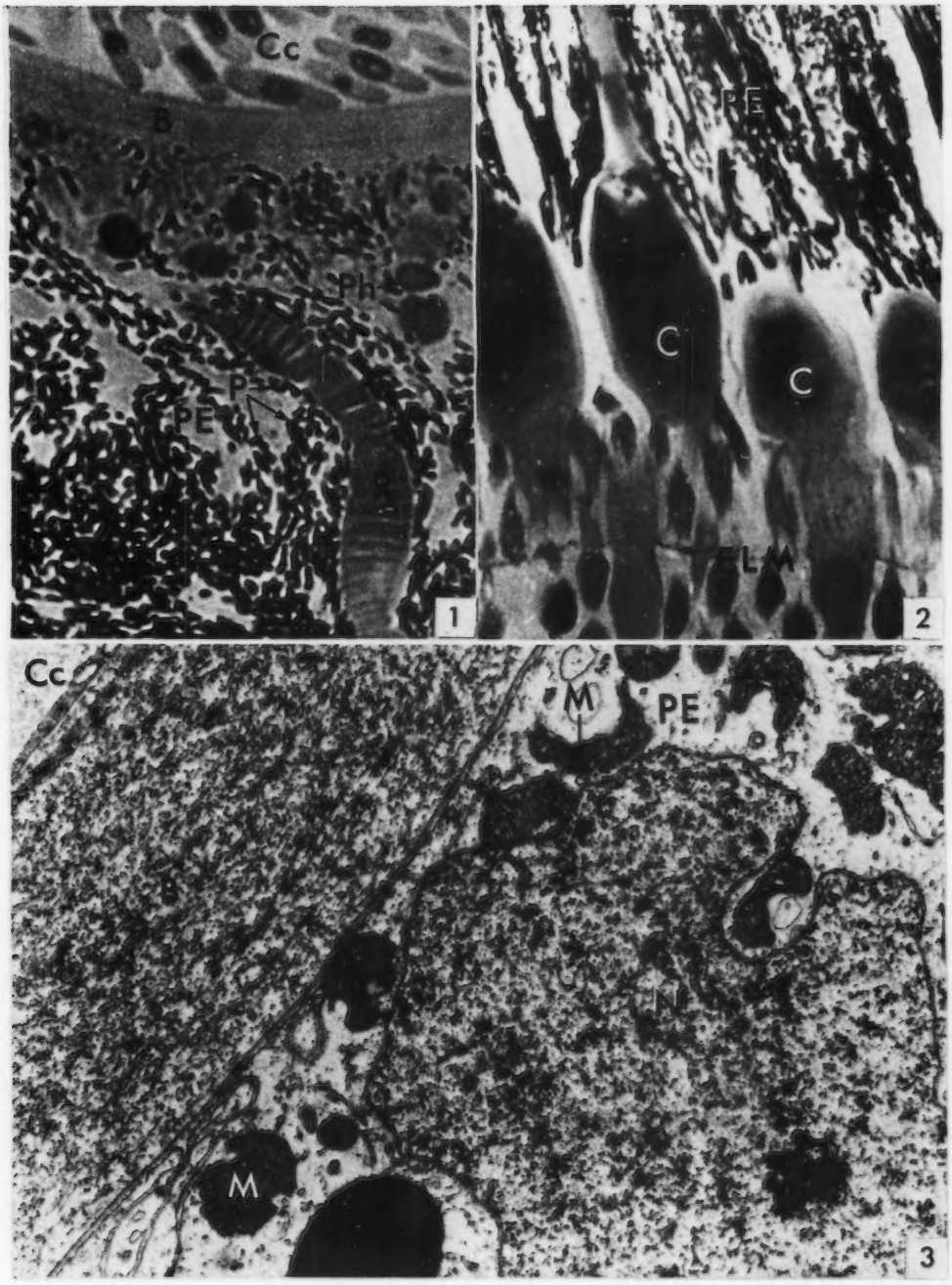
The nucleus of a pigment epithelial cell is large, of an irregular shape, and located at the base of the cell (Fig. 3). Numerous irregularly shaped mitochondria are also found in the basal region (Fig. 3,4). Small amounts of rough endoplasmic reticulum and polysomes are distributed throughout the epithelial cell (Fig. 3,4,7). Smooth endoplasmic reticulum is more abundant and is generally located in the apical region of the cell (Fig. 6). Phagosomes are a common feature of these cells (Fig. 7). Myeloid bodies of various shapes are also found in the apical cytoplasm (Fig. 5,6). The cisternae of the myeloid bodies can often be seen to be continuous with the cisternae of the smooth endoplasmic reticulum (Fig. 6).

The scleral or basal surfaces of the pigment epithelial cells are mostly smooth (Fig. 3,4,7), with only rare infoldings, usually where adjacent epithelial cells meet basally (Fig. 4). The lateral cell borders are moderately infolded and joined by junctional complexes (zonulae occludentes) (Fig. 4). The apical region of the epithelial cell displays numerous long, slender processes (Fig. 2). These processes contain numerous pigment granules and closely invest the inner and outer segments of the photoreceptors (Fig. 2,5). In the light-adapted condition, the pigment granules are located predominantly in the apical two-thirds of the cell (Fig. 1,2).

Bruch's Membrane

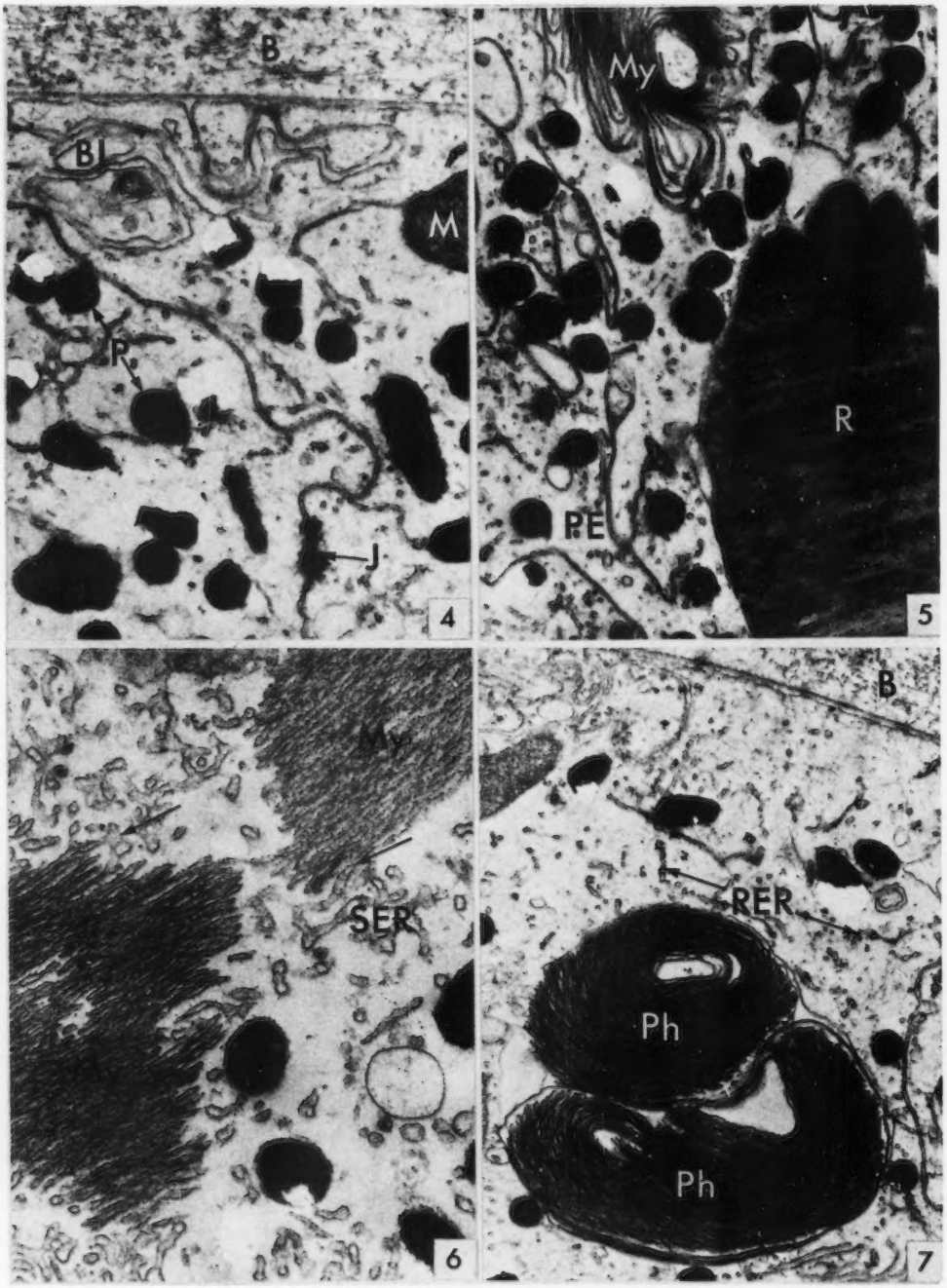
Bruch's membrane in the northern pike is a relatively thick (average 3.5–4 μ posteriorly) multilayered structure between the choroid and neural retina (Fig. 3). Its innermost (or vitreal) component is the basal lamina of the pigment epithelial layer (Fig. 3,4,7). Its most scleral edge is marked by the less well-developed basal lamina of the choriocapillaris endothelium (Fig. 3,9,10). The bulk of Bruch's membrane lies between these basal laminae and is composed of a three-dimensional meshwork of fine fibrils (Fig. 2,4,10,11) which do not display conspicuous cross-striations.

The substance of Bruch's membrane occasionally invades the pigment epithelial layer as a thickening that invaginates between the epithelial cells (Fig. 8). In these regions, the invasive portion of Bruch's membrane appears relatively amorphous (Fig. 8). In all cases, these invaginations are separated from the epithelial cells by the basal lamina (Fig. 8). Similarly on the choroidal side, the substance of Bruch's membrane can occasionally be seen to invaginate between overlapping endothelial processes to lie very close to the lumen of the choriocapillaris (Fig. 11). In these regions the endothelial basal lamina is usually absent (Fig. 11). No central lamina



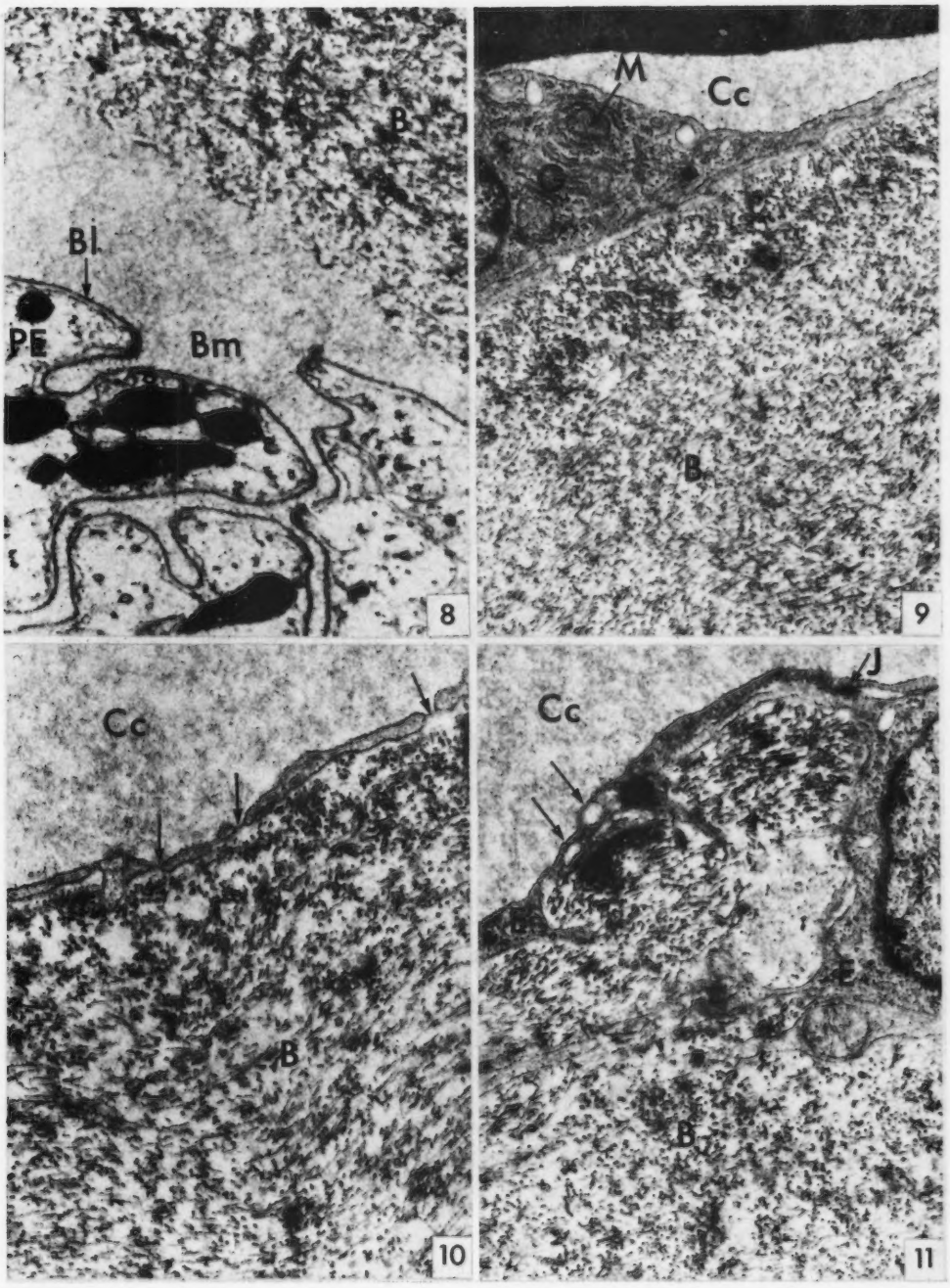
FIGURES 1–3

FIG. 1. Light micrograph showing the choriocapillaris (Cc), Bruch's membrane (B), and a portion of the pigment epithelial layer (PE) in an adult northern pike (*Esox lucius*). A portion of a rod outer segment (R), phagosomes (Ph), and pigment granules (P) are also indicated. ×3500; FIG. 2. Light micrograph showing the apical projections of the pigment epithelial cells (PE) reaching to the inner segments of the photoreceptor cells. Two cone photoreceptors (C) and the external limiting membrane (ELM) are indicated. ×3500; FIG. 3. Electron micrograph illustrating the basal region of a pigment epithelial cell (PE). The nucleus (N) as well as the mitochondria (M) are irregular in shape. Note the scarcity of basal infoldings. Bruch's membrane (B) is seen as a thick collagenous layer. No fenestrations are seen in the endothelium of the choriocapillaris (Cc). ×18,000.



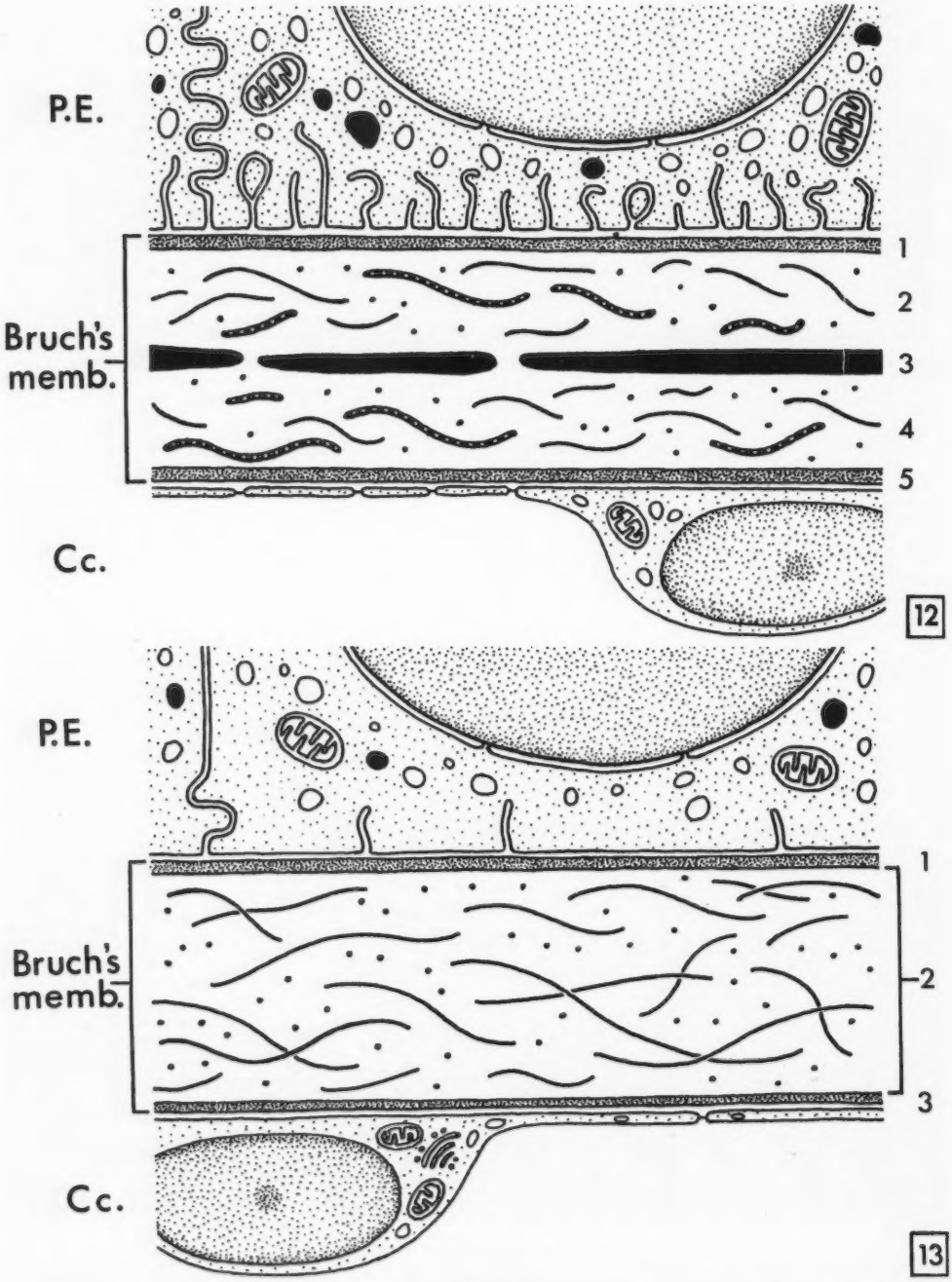
FIGURES 4–7

FIG. 4. Electron micrograph of the basal region of a pigment epithelial cell. Basal infoldings (B1) are present at the lateral cell borders. A lateral cell junction (J), mitochondrion (M), and pigment granules (P) are indicated. Bruch's membrane (B) is at the top. ×22,800; FIG. 5. Electron micrograph of the apical region of a pigment epithelial cell. Pigment laden processes (PE) surround a rod outer segment (R). A portion of a myeloid body is also seen (My). ×18,000; FIG. 6. Electron micrograph of portions of two myeloid bodies (My) in the apical cytoplasm of a pigment epithelial cell. They can be seen to be continuous (arrows) with the smooth endoplasmic reticulum (SER). ×32,500; FIG. 7. Electron micrograph showing two membrane-bound phagosomes (Ph). Small amounts of rough endoplasmic reticulum (RER) are also seen. Bruch's membrane (B) is at upper right. × 16,500.



FIGURES 8–11

FIG. 8. Electron micrograph of the basal region of a pigment epithelial cell to illustrate the invagination of Bruch's membrane material (Bm) into the pigment epithelium (PE). Bruch's membrane proper (B) is seen at upper right. The basal lamina (Bl) of the pigment epithelium is indicated. ×18,000; FIG. 9. Electron micrograph of Bruch's membrane (B) and the choriocapillaris (Cc). The endothelial cells lack fenestrae but are rich in organelles. A Golgi zone (G) and mitochondrion (M) are indicated. An erythrocyte is seen at the top. ×21,000; FIG. 10. Electron micrograph of the choriocapillaris (Cc) and Bruch's membrane to show that endothelial fenestrations (arrows) are occasionally seen. ×32,000; FIG. 11. Electron micrograph of Bruch's membrane (B) and the choriocapillaris (Cc). Bruch's membrane has invaginated between the endothelial cell processes (E). A tight junction is indicated (J) as are vesicles in the endothelial processes (arrows). ×27,000.



FIGURES 12–13

FIG. 12. Characteristic features of choriocapillaris region in a "typical" vertebrate. Numerous basal infoldings are seen in the pigment epithelial cell. Bruch's membrane has five distinct layers and numerous fenestrations are seen in the choriocapillaris (modified from Nakaizumi); FIG. 13. Morphology of choriocapillaris region in the northern pike. Very few basal infoldings are seen in the pigment epithelial cells. Bruch's membrane lacks a central lamina densa and is composed of only three layers. Very few endothelial fenestrations are present.

densa is seen within Bruch's membrane of the northern pike (Fig. 3).

Choriocapillaris

The endothelial wall of the choriocapillaris of the northern pike is typically thin but nonfenestrated where it borders Bruch's membrane (Fig. 3,9,11). Occasionally, regions of the choriocapillaris can, however, be found which display endothelial fenestrations bridged by a diaphragm (Fig. 10).

The endothelial cell processes often overlap and are bound together by tight junctions (Fig. 11). Vesicles are common within the endothelial cytoplasm where no fenestrations are found (Fig. 3,11). The nuclear region of the endothelial cells is rich in cell organelles; particularly Golgi zones, mitochondria, and rough endoplasmic reticulum (Fig. 9).

Figure 12 summarizes the essential morphological features of this region in vertebrates other than the northern pike; those of the northern pike are shown in Fig. 13.

Discussion

Pigment Epithelium

In most adult vertebrates described, the basal region of the pigment epithelial cells is highly infolded and contains numerous mitochondria (Iwaki 1959; Garron 1963; Dowling and Gibbons 1962; Dickson and Hollenberg 1971). These morphological features are assumed to indicate an active role in fluid transport by these cells (Porter and Yamada 1960; Dowling and Gibbons 1962). Okuda (1962) has indicated an absence of basal infoldings in the frog and a fish (*Cyprinus carassius*). Although the pigment epithelial cells of the northern pike do contain numerous mitochondria, basal infoldings are not frequent and this perhaps indicates that the rate of fluid transport is less in the pike than in other vertebrates that do display prominent basal infoldings.

The preponderance of smooth endoplasmic reticulum over rough endoplasmic reticulum and polysomes has been noted elsewhere (Yamada 1961; Leure-du Pree 1968). The presence of large amounts of smooth endoplasmic reticulum has also been noted in other pigment epithelia (Porter and Yamada 1960; Dickson and Hollenberg 1971) and in cells involved in steroid biosynthesis (Enders 1962). It is known that the pigment epithelium is active in vitamin A storage and in the synthesis of lipoid photopigment precursors (Dowling 1960).

Both phagosomes and myeloid bodies have been reported in other species (Kroll and Machemer 1968; Dickson and Hollenberg 1971; Marshall and Ansell 1971). Phagosomes are known to be portions of degenerating rod photoreceptor outer segments, which are phagocytosed by the epithelial cells (Young 1968, 1969; Young and Droz 1968; Kroll and Machemer 1968, 1969). In the human eye, Spitznas and Hogan (1970) have noted two types of pigment epithelial cell processes and have described an active process whereby the apical portions of rod outer segments are removed by these pigment epithelial processes. Myeloid bodies are large arrays of membranes not bounded by a limiting membrane (Cohen 1969; Marshall and Ansell 1971). These structures are often seen to be continuous with the cisternae of the smooth endoplasmic reticulum (Porter and Yamada 1960; Yamada 1961) and even with the nuclear envelope and outer mitochondrial membrane (Hazlett et al. 1973). The myeloid body, unlike the phagosome, is not reported in all species and, as yet, has no function ascribed to it.

The series of lateral cell junctions between the epithelial cells is also a common feature (Fine 1961; Leure-du Pree 1968). Cohen (1965) has suggested that this terminal bar system constitutes an effective barrier to extracellular transport. As in other species, the concentration of pigment granules in the apical cytoplasm in the light-adapted condition probably aids in the absorption of incident light to prevent scatter and hence improve visual acuity (Moyer 1969). The pigment epithelial layer in the northern pike is exceptionally thick and as Polyak (1957) has indicated, comprises about one-fifth of the thickness of the whole retina.

Bruch's Membrane

Bruch's membrane in other vertebrates is typically described as a pentalaminate structure (Sumita 1961a, 1961b; Nakaizumi 1964a, 1964b; Hollenberg and Burt 1969; Hogan et al. 1971). The five layers are the basal lamina of the pigment epithelial layer (layer 1 — see Fig. 12) and the basal lamina of the choriocapillaris (layer 5) enclosing a central discontinuous lamina densa (layer 3) and an inner (layer 2) and outer (layer 4) collagen layer.

Only a few exceptions to this pentalaminate structure have previously been reported. Nakaizumi (1964a) found that in eyes with a choroidal tapetum, Bruch's membrane over the tapetal area consisted only of the two basal laminae that formed layers 1 and 5 in the normal condition. In such a region, the pigment epithelial cells retained their basal infoldings and the choriocapillaris kept its fenestrations. Interestingly, in the cow, which has a fibrous tapetum, Bruch's membrane does not change over the tapetal area (Nakaizumi 1964b).

Okuda (1962) briefly reported that in the eel no definite structure could be observed within Bruch's

membrane and that in *Cyprinus carassius*, many thin lamellae were seen in Bruch's membrane instead of collagen fibrils.

Bruch's membrane in the pike is much thicker than previously reported in other vertebrates. The average thickness of this structure at the posterior pole of the human eye is .86–2.06 μ, of the monkey eye is .40–1.36 μ, and of the rat eye is .32–1.62 μ (Nakaizumi 1964a). In the pike, it averages 3.5–4 μ in this location. This increased thickness of Bruch's membrane may indicate a greater barrier to diffusion of fluids from the pigment epithelium than is present in other vertebrates.

The inner edge of Burch's membrane (layer 1) in the pike, as in other species, is the basal lamina of the pigment epithelium (Sumita 1961a, 1961b; Nakaizumi 1964a; Hollenberg and Burt 1969). The outer edge (layer 3) is formed by a less well-defined and, often discontinuous, basal lamina of the choriocapillaris (Sumita 1961a). No central lamina densa is seen in the pike as is reported for other vertebrates (Hogan et al. 1971). Because of the lack of a lamina densa, a single, thick layer of fibrils forms the bulk of Bruch's membrane in the pike (layer 2 — Fig. 13).

The origin of the fine fibrils in layer 2 is not known. The pigment epithelial cells would appear to contain too little rough endoplasmic reticulum to produce such an array of fibrils. It is possible that the endothelial cells and intercapillary choroidal fibroblasts are the source of this material.

The significance of the areas of invagination of the pigment epithelium by Bruch's membrane is not clear but they may facilitate transport of materials to the pigment epithelium. In the same manner, Bruch's membrane insinuated between endothelial processes would allow a close apposition of this layer to the choriocapillaris and, perhaps, aid transport. Aging changes may also lead to thickenings of Bruch's membrane that protrude between the basal infoldings of the pigment epithelium (Hollenberg and Burt 1969). However, in such cases the additional thickenings usually contain much electron-dense material that is not seen in the thickenings of Bruch's membrane in the pike.

Choriocapillaris

The capillaries of the choriocapillaris in most vertebrates have a fairly large lumen (Bernstein 1960, 1961; Leeson and Leeson 1967), which is indicative of a slow blood velocity. Also in other vertebrates, the endothelial wall of the choriocapillaris facing Bruch's membrane is very highly fenestrated (Bairati and Orzalesi 1963; Bernstein and Hollenberg 1965b). These structural characteristics point to the movement of large volumes of fluid, as well as the passage of relatively large molecules (Bernstein and Hollenberg 1965a, 1965b).

The choriocapillaris of the pike has a large lumen but the endothelial wall, although very thin, is not typically fenestrated. Pinocytotic vesicles, however, appear to be more common in the endothelium of the choroidal capillaries of pike than in most other species, and sufficient transport of metabolites may occur by pinocytosis.

In conclusion, the choriocapillaris, Bruch's membrane, and pigment epithelium in the pike eye do not display the morphology indicative of rapid diffusion, i.e. highly fenestrated endothelium and basally infolded epithelia. It is, however, well established that the choriocapillaries supply a major portion of the metabolites to the outer retina (Bernstein 1960, 1961; Bernstein and Hollenberg 1965a). Wittenberg and Wittenberg (1974) have recently stated that the choroid rete mirabile (or choroid gland) of the teleost eye is specifically adapted to deliver a large flow of oxygen to the retina. Presumably, therefore, the presence of a large choroid rete mirabile in the pike eye and pinocytotic transport coupled with the lack of a lamina densa is sufficient to supply at least the outer portion of this retina, which is itself avascular. Tracer studies may indicate more clearly the volume and rapidity of diffusion in this region of the pike eye.

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Role of Olfaction and Vision in the Behavior of American Shad (*Alosa sapidissima*) Homing to the Connecticut River from Long Island Sound

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DODSON, J. J., AND W. C. LEGGETT. 1974. Role of olfaction and vision in the behavior of American shad (*Alosa sapidissima*) homing to the Connecticut River from Long Island Sound. J. Fish. Res. Board Can. 31: 1607–1619.

Twenty-two adult American shad (*Alosa sapidissima*), captured, sensory-impaired, sonic-tagged, and released adjacent to and 10 km west of the Connecticut River, were tracked in Long Island Sound in 1972. Both anosmic and blind/anosmic shad oriented into the tidal current and altered swimming speeds in relation to changes in tidal current velocity as do unimpaired fish. They did not, however, exhibit the consistency in these behavioral responses that resulted in westerly displacement in unimpaired shad. Blind shad exhibited neither of these behavior patterns but did tend to affect a westerly displacement in Long Island Sound.

Dart-tagged adult shad that were sensory-impaired and released without displacement in the same areas of Long Island Sound in 1971 and 1972 homed less successfully to the Connecticut River than did unimpaired dart-tagged shad released in the same years. Anosmic dart-tagged shad located the Connecticut River less successfully than unimpaired shad. Blind shad successfully located the river from 10 km distance but failed to do so when released adjacent to the river. Blind/anosmic shad failed to locate the river from either release site.

It was concluded that an olfactory–rheotaxic mechanism forms the basis of the location of the Connecticut River by shad. The preferred direction of displacement appears to be established by olfactory clues indicative of the Connecticut River whereas the orientation along the migratory path is maintained by reference to the rate and direction of tidal currents. Vision alone cannot account for this rheotaxic response.

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Vingt-deux aloses savoureuses (*Alosa sapidissima*) adultes, capturées, rendues aveugles et anosmiques, équipées de marques ultrasonores et relâchées à proximité et à 10 km de la rivière Connecticut, ont été suivies dans le détroit de Long Island en 1972. Les aloses anosmiques, de même que les aloses aveugles/anosmiques se sont orientées dans le courant de marée et ont modifié leur vitesse de nage en réponse aux changements de vitesse du courant, tout comme les poissons intacts. Leurs réponses ne furent toutefois pas aussi uniformes que celles qui ont amené les aloses intactes à se déplacer vers l'ouest. Les aloses aveugles ne montrèrent aucun de ces modes de comportement, mais eurent tendance à se déplacer vers l'ouest dans le détroit de Long Island.

Les aloses adultes marquées de dards, dont les sens avaient été altérés et qui avaient été relâchées sans déplacement dans les mêmes régions du détroit de Long Island en 1971 et 1972, eurent moins de succès à retourner à leur rivière d'origine, la rivière Connecticut, que les aloses intactes marquées de dards et relâchées ces mêmes années. Les aloses anos-

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miques marquées de dards eurent moins de succès à trouver la rivière Connecticut que les aloses intactes. Les aloses aveugles réussirent à localiser la rivière Connecticut d'une distance de 10 km, mais ne purent le faire lorsque libérées dans le voisinage de la rivière. Les aloses aveugles/anosmiques ne réussirent pas à localiser la rivière de l'un ou de l'autre site de remise à l'eau.

Nous en concluons qu'un mécanisme olfactif–rhéotactique permet à l'alose de localiser la rivière Connecticut. La direction préférée du déplacement semble être déterminée par des indices olfactifs conduisant à la rivière Connecticut, alors que l'orientation le long de la voie de migration est maintenue par référence à la vitesse et à la direction du courant de marée. La vision seule ne peut expliquer cette réponse rhéotactique.

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THE American shad (*Alosa sapidissima*), largest member of the herring family (Clupeidae), is native to the eastern coast of North America. It is anadromous, undertakes extensive oceanic migration, and returns to its natal river to spawn (Walburg and Nichols 1967). Dodson and Leggett (1973) demonstrated that adult shad native to the Connecticut River, and migrating in Long Island Sound during the final saltwater stages of the spawning migration, located their home river by means of an extensive nonrandom search. We hypothesized that environmental clues indicative of the Connecticut River acted to establish the westerly bias in the open water orientation of shad in Long Island Sound, while the actual displacement was achieved by adjusting swimming speeds and headings in response to changes in the rate and direction of tidal currents. This paper reports the results of studies designed to test this hypothesis and to identify the environmental clues instrumental in establishing and directing this behavior.

Materials and Methods

ULTRASONIC TRACKING

Twenty-two adult shad (45–55 cm) were tagged internally with ultrasonic transmitters, released without displacement, and tracked in Long Island Sound (Fig. 1) during April, May, and June, 1972. The tags had a pulsed output ranging from 60–200 pulses/min, a frequency of 70 kHz, a maximum range of 30–300 m, and an effective life of 15 days. They were housed in polystyrene cylinders 6.4 cm long and 1.3 cm in diameter; their weight in air was 14.5 g. The receiving unit was a portable receiver (Smith-Root model TA-60) tunable in the range 60–180 kHz coupled to a hydrophone having a peak frequency of 70 kHz and a cone of reception of approximately 15°. Swimming depth of the tracked fish was unknown.

All fish were captured with 14-cm (stretch measure) monofilament gillnets. Capture was signalled by movement of the headrope floats and the fish were immediately removed by cutting the mesh holding the fish.

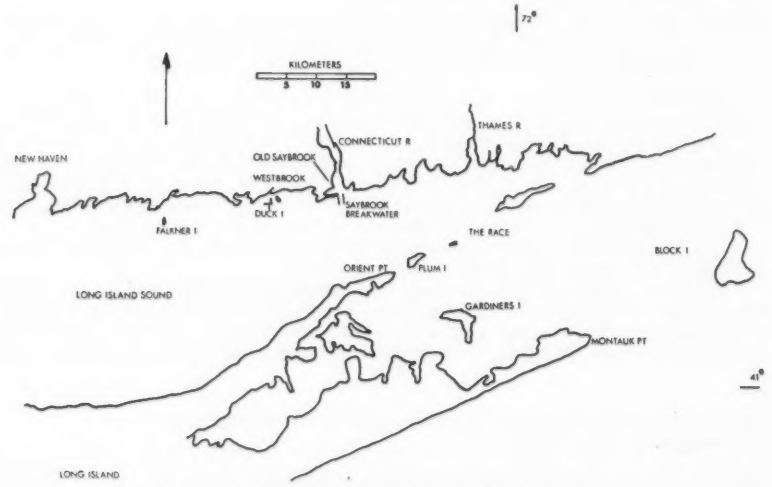

FIG. 1. Location map of Long Island Sound.

If the fish was undamaged by capture a sonic tag was inserted into the stomach via the mouth.

Seven shad were blinded by injection of 3% benzethonium chloride (Phemerol, Parke Davis and Co.) into the eyeball (McCleave 1967). Tests conducted in a live car anchored in salt water demonstrated that shad treated in this way lost sight within 1 h. Loss of sight was indicated by the eye turning white in color and by the increased frequency of fish colliding with the sides of the car. Eight shad were olfactory occluded by injection of silicone sealant (Dow Corning) into the nares. The sealant was sufficiently dense to block the entrance of water into the nares and had adequate viscosity to fill every fold of the nasal cavity. Shad heads treated in this way and left in violently running water for 48 h lost no plugs. On dissection, the plugs were observed to overlay the sensory epithelium completely. Seven shad were both blinded and olfactory occluded. Following insertion of the tag and sensory impairment, all fish were gently returned to the water without displacement. Total time from capture to release was less than 2 min in all cases.

Releases were made at two sites in Long Island Sound: a) Westbrook, (72°28′, 41°16′) — three blind shad, four olfactory occluded (anosmic) shad, three blind/anosmic shad; b) west side of the Saybrook breakwater (72°20′, 41°15′50″) — four blind shad, four anosmic shad, four blind/anosmic shad (Fig. 1).

Movements of sonic-tagged fish were monitored by immediate and continuous tracking from a 6.4-m boat which was maintained behind and in line with the tagged fish. This was possible due to the directivity of the manually rotated hydrophone. The distance between the fish and the boat was estimated by changes in incoming signal strength which was roughly calibrated for each tag prior to release. The position of the fish (accurate to within 50 m) was obtained at least every 30 min by triangulation using navigation aids and prominent shore features. When possible, cloud cover, wind strength and direction, wave condition, tidal condition, depth, temperature and salinity (measured at 2-m depth increments), and boat speed through the water were recorded coincident with fish position. Temperature and salinity were measured with a Hydrolab TC-2 conductivity meter. Boat speed through the water was measured with a Gurly flowmeter.

The portion of the data associated with open water migration, i.e. not associated with fish movements about breakwaters, islands, and similar obstructions, was extracted from the main body of data and analyzed. The first hour of individual tracks was excluded from the analysis to avoid incorporating nonsense behavior arising from possible temporary disorientation due to handling.

Long Island Sound experiences a reversing tidal current which floods to the west and ebbs to the east. The movement of sonic-tagged shad in Long Island Sound thus resulted from the combined effects of the rate and direction of the tidal current and the heading and swimming speed of the fish. Data on tidal rate and direction during the tracks were available from our records and from tidal tables and charts for Long Island Sound. These data were combined and used together with observations of fish movement over time to calculate fish heading and swimming speed through the water using triangulation and vector velocity techniques. Swimming speeds determined in this way are referred to as "calculated swimming speeds" and represent the minimum speed at which a fish must swim to travel a straight line between two points in a given increment of time. This calculation tends to underestimate the actual swimming speed since straight line courses were seldom followed.

Current velocity values presented in the tidal charts and tables for Long Island Sound were derived from measurements made to a depth of 6 m (U.S. Coast and Geodetic Survey). As the depth of tracked shad could not be measured, a knowledge of differences in current velocity throughout the water column was necessary to assess the accuracy of swimming speed calculations. Riley (1956) reported that at midtide, when current velocities are maximum, the velocity of the flood (westerly) tide remains relatively constant throughout the water column, whereas the ebb (easterly) tide velocity is greater at the surface than at the bottom (30 m). Thus swimming speeds calculated during ebb tide conditions may be overestimated if the fish were swimming deeper than 6 m. To avoid this possible source of error, swimming speeds calculated under different tidal conditions were not directly compared. Rather, swimming speeds were only analyzed relative to tidal velocity.

Swimming speeds were also estimated by observing the speed of the boat through the water as the fish moved from one point to the next along the track. These "observed swimming speeds" are also subject to some error since it was not possible to accurately integrate the range of the entire ½-h period of these speeds observed. They do, however, provide a reasonable approximation to average swimming speeds between successive positions along the track.

Arithmetic means were used to calculate mean fish headings during each tidal condition because the range of observed headings during each tidal cycle was less than 180°. Batschelet (1965) reported that such distribution can be considered linear and that under such conditions arithmetic means differ little from angular means. Mean headings were classified as countercurrent (fish heading $<45° \pm$ reciprocal of tide heading), concurrent (fish heading $<45° \pm$ tide heading), and crosscurrent (all headings other than those described).

Precision of unidirectional orientation under different conditions of tide and sensory impairment were analyzed by calculating the frequency of large turning angles ($>45°$) observed under these conditions (Madison et al. 1972; Dodson and Leggett 1973).

All analyses were carried out on combined data from each impairment category. Individual tracks were similarly analyzed if the track duration extended through at least one full tidal cycle. The behavior of sensory-impaired shad observed in this study was compared with that of unimpaired shad tracked in 1970 and 1971 (Dodson and Leggett 1973).

Conventional Tagging

In 1971, 231 blind shad, 220 anosmic shad, and 312 unimpaired shad were externally marked with nylon dart tags and released without displacement from the same areas of Long Island Sound as the sonic-tagged shad. Olfactory occlusion was achieved by injecting the nares with vaseline and cotton plugs (Wisby and Hasler 1954). This procedure proved unsatisfactory and the data for dart-tagged anosmic shad released in 1971 were discarded. Blinding was effected by the method previously outlined for sonic-tagged shad.

In 1972, 141 blind shad, 143 anosmic shad, 128 blind/anosmic shad, and 150 unimpaired shad were dart-tagged and released at these sites. Olfactory occlusion of this group was by injection of silicone sealant into the nares as previously described.

Differences in the frequency of recovery of sensory-impaired and sensory-intact dart-tagged shad in the Connecticut River were used as a measure of the relative ability of the four groups to locate the river following release.

Results

Conventional Tagging

The frequencies of recovery, in the Connecticut River, of impaired and unimpaired dart-tagged shad are presented in Table 1. Blind and unimpaired shad released at Westbrook homed to the Connecticut River equally well from Westbrook. Blind shad released at Saybrook had a reduced homing success as compared with unimpaired shad. Anosmic shad were generally less successful than unimpaired shad in locating the river from both release areas. Three anosmic shad were captured far from the Connecticut River; one at Gardiner's Island and two at Montauk Point (Fig. 1). Blind/anosmic shad failed completely to locate the Connecticut River.

The recovery frequency of unimpaired shad released in Long Island Sound in 1971 and 1972 did not differ significantly ($\chi^2 = 0.33$, $P>0.1$). Furthermore, the recovery frequency of these shad did not differ significantly from the recovery of 8769 dart-tagged unimpaired shad released in the Connecticut River proper in 1971 and 1972 ($\chi^2 = 1.83$, $P>0.1$).

The mean homing time of dart-tagged sensory-intact shad released at Westbrook in 1971 (7.9 days, SD= 6.7, n= 25) and in 1972 (7.6 days, SD= 4.6, n=6) was not significantly different (t= 0.10, $P>0.1$). Similarly, the mean homing time of dart-tagged sensory-intact shad released at Saybrook in 1971 (5.2 days, SD= 4.9, n= 20) and in 1972 (6.3 days, SD= 6.3, n= 11) was not significantly different (t= 0.54, $P>0.1$).

Ultrasonic Tracking

Paths of migration — Six of eight anosmic shad were tracked continuously after release in Long Island Sound (Fig. 2). Of the two remaining, one was lost immediately due to equipment failure and one failed to move suggesting that either the tag was regurgitated or the fish died after release. Anosmic shad 2 and 4 moved to the west during both ebb and flood tides whereas anosmic shad 1 and 3 moved to the east during both tidal conditions. Anosmic shad 5 and 6 moved to the west during the flood tide and to the east during the ebb tide.

Five of seven blind shad were tracked continuously after release (Fig. 3). Two were lost immediately after release due to poor weather

Table 1. Frequency of recovery in the Connecticut River of impaired and unimpaired dart-tagged American shad (*Alosa sapidissima*) released in Long Island Sound in 1971 and 1972. Chi-square values obtained from comparisons of recovery frequencies of each category of impaired shad with that of unimpaired shad. 5% probability level = 3.84.

		1971		1972		Combined		
Release area	Fish treatment	no. released	no. recap.	no. released	no. recap.	no. released	no. recap.	χ^2
Saybrook	Unimpaired	206	35	115	17	321	52	
	Blind	166	11	109	6	275	17	14.52
	Anosmic	–	–	111	10	111	10	3.47
	Blind/anosmic	–	–	97	0	97	0	×
Westbrook	Unimpaired	106	23	35	7	141	30	
	Blind	65	11	32	6	97	17	.61
	Anosmic	–	–	32	3	32	3	2.39
	Blind/anosmic	–	–	31	0	31	0	×

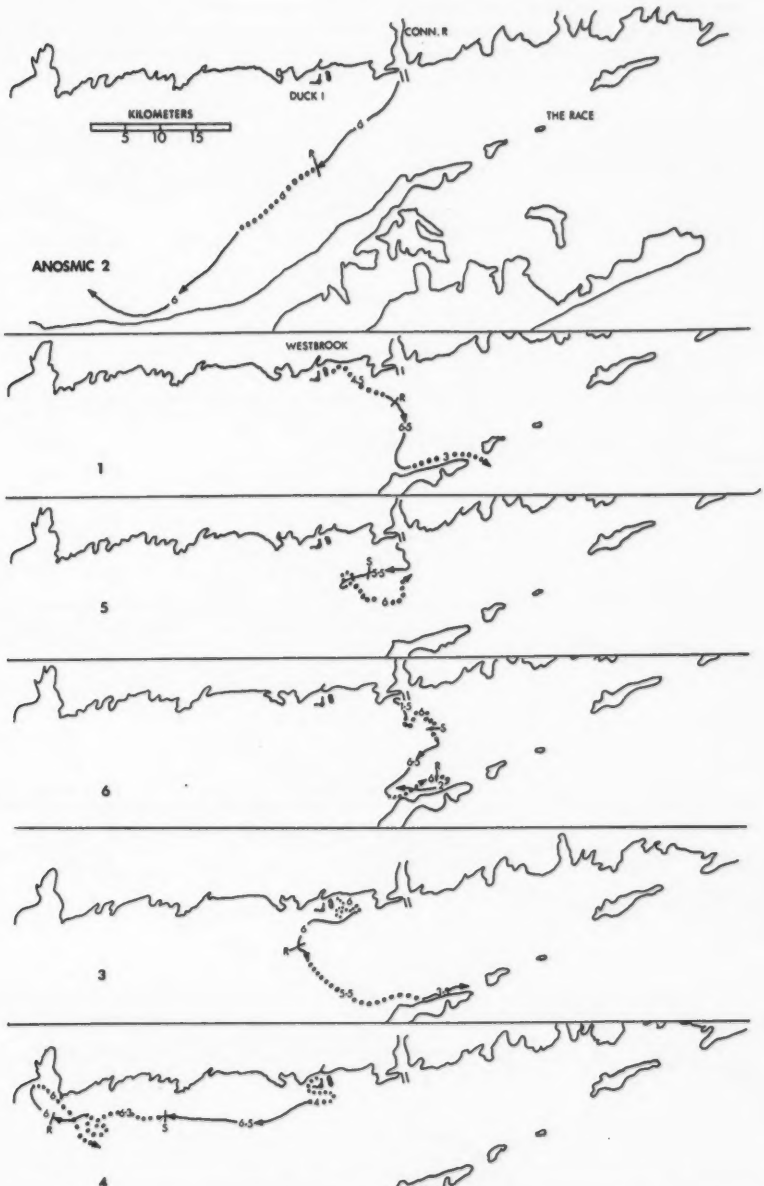

FIG. 2. Migration routes of six anosmic sonic-tagged American shad (*Alosa sapidissima*) tracked in Long Island Sound in 1972. Solid line represents fish displacement during flood tide, dotted line during ebb tide. Numbers represent time in hours during the indicated tidal condition. R — point of observed sunrise; S — point of observed sunset.

conditions. Blind shad 2, 3, and 5 all moved west during both tidal conditions, blind shad 4 moved east during both tidal conditions, and blind shad 1 moved east during ebb tide and west during flood tide.

Five of seven blind/anosmic shad were tracked continuously following release (Fig. 4). Of the remaining two, one was lost due to poor weather conditions and one was lost due to equipment

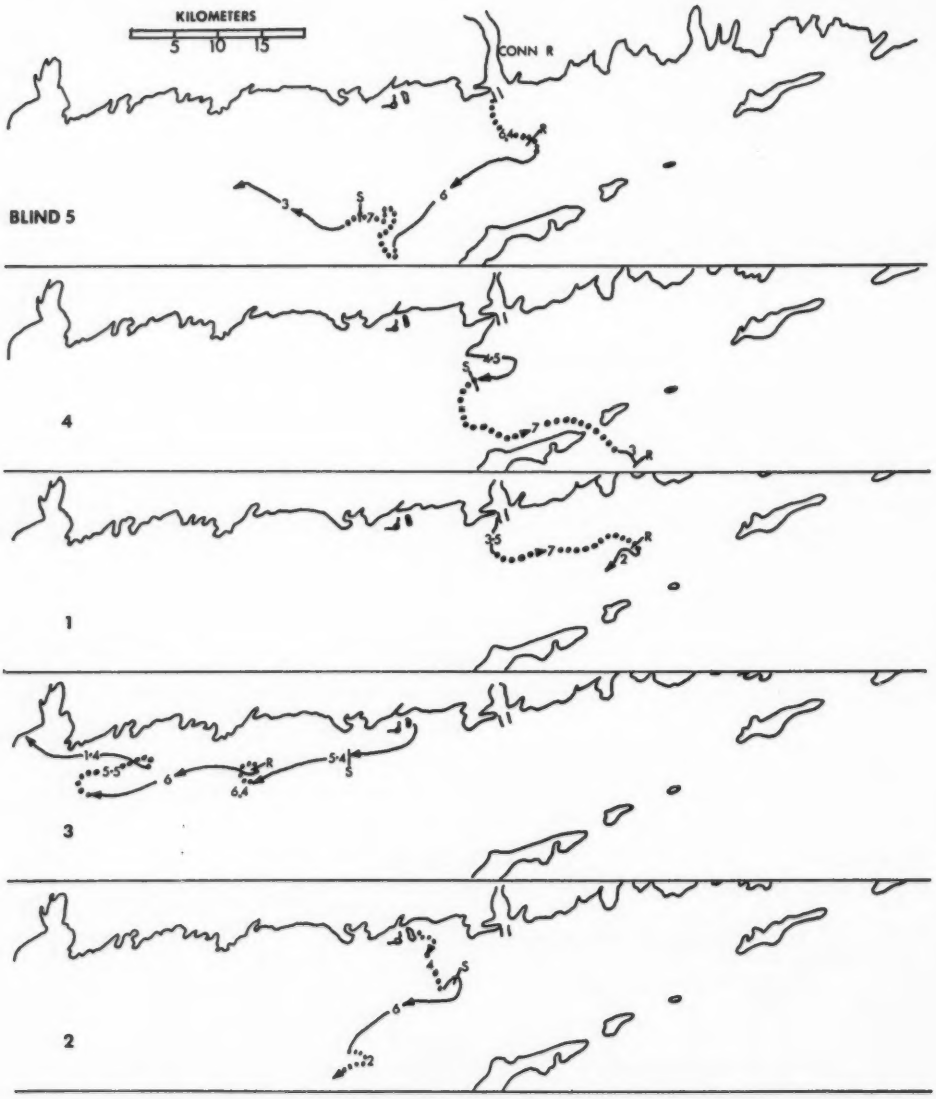

FIG. 3. Migration routes of five blind sonic-tagged shad tracked in Long Island Sound in 1972. Solid line represents fish displacement during flood tide, dotted line during ebb tide. Numbers indicate time in hours during the indicated tidal condition. R — point of observed sunrise; S — point of observed sunset.

failure. Blind/anosmic shad 1 moved west during both tides while the remaining four moved west during flood tide and east during ebb tide.

Behavior — Response to tidal current direction — Current directions and headings of sensory impaired shad were calculated over 15-and 30-min

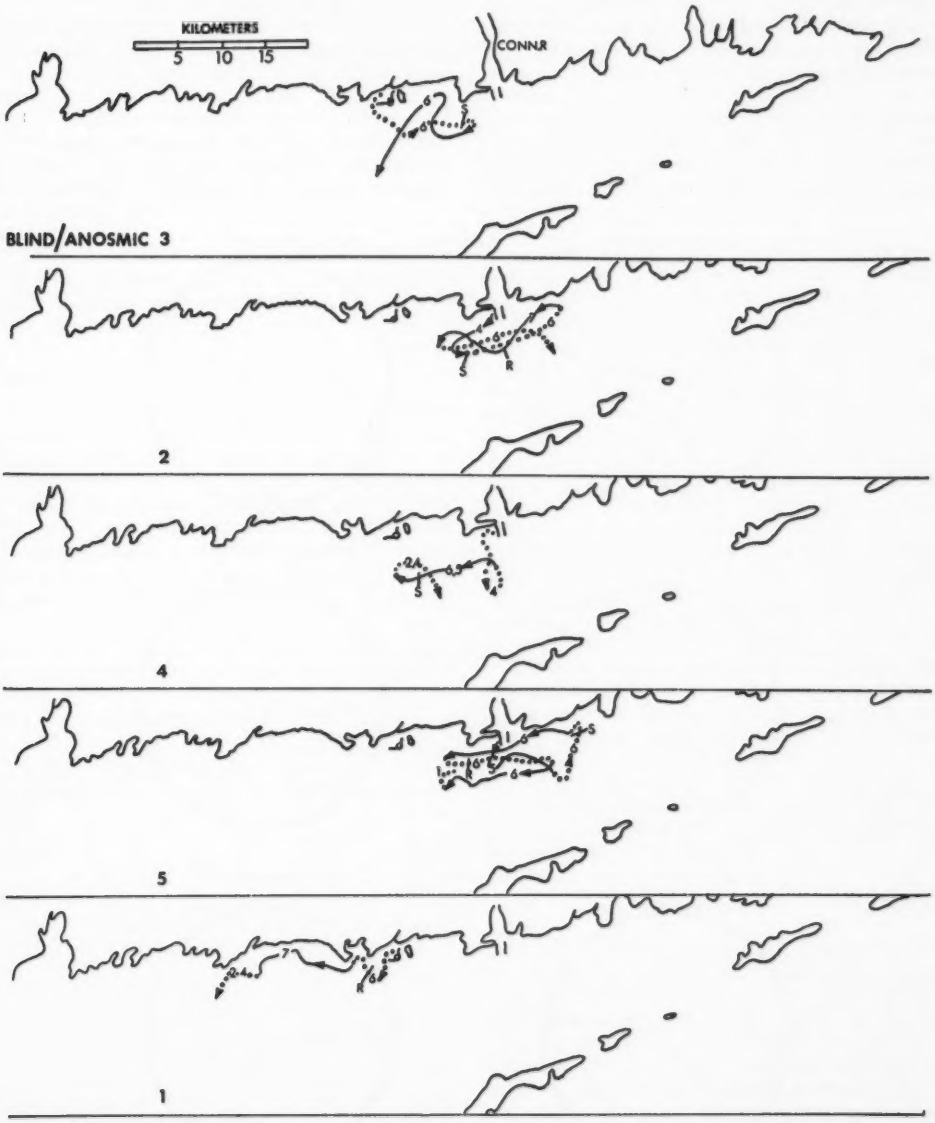

FIG. 4. Migration routes of five blind/anosmic sonic-tagged shad tracked in Long Island Sound in 1972. Solid line represents fish displacement during flood tide, dotted line during ebb tide. Numbers represent time in hours during the indicated tidal condition. R — point of observed sunrise; S — point of observed sunset.

time increments and the data for each category of sensory-impaired shad was pooled. Anosmic shad headings and current directions were negatively correlated ($r = -0.25$, $n = 213$, $P<0.01$). This tendency to orient into the reversing tide was equally significant during daylight and darkness. Blind shad headings and current directions were not significantly correlated ($r = -0.08$, $n = 142$, $P>0.1$). Blind/anosmic shad headings and current directions were negatively correlated ($r= -0.25$, $n= 194$, $P<0.01$). The tendency of blind/anosmic shad to orient into the current was more significant during daylight ($r= -0.27$, $n= 122$, $P<0.01$) than darkness ($r= -0.16$, $n= 72$, $P>0.1$). Mean fish headings during ebb and flood tide conditions were plotted against mean ebb and flood tide current directions and are shown for each category of sensory-impaired shad in Fig. 5.

Changes in the headings of impaired shad at successive positions along the tracks (turning angles) were calculated for each shad tracked in 1972 and analyzed within each category of sensory impairment for the frequency of large turning angles (>45°) exhibited during ebb and flood tide conditions. The pooled data for each impairment category revealed no significant differences in the

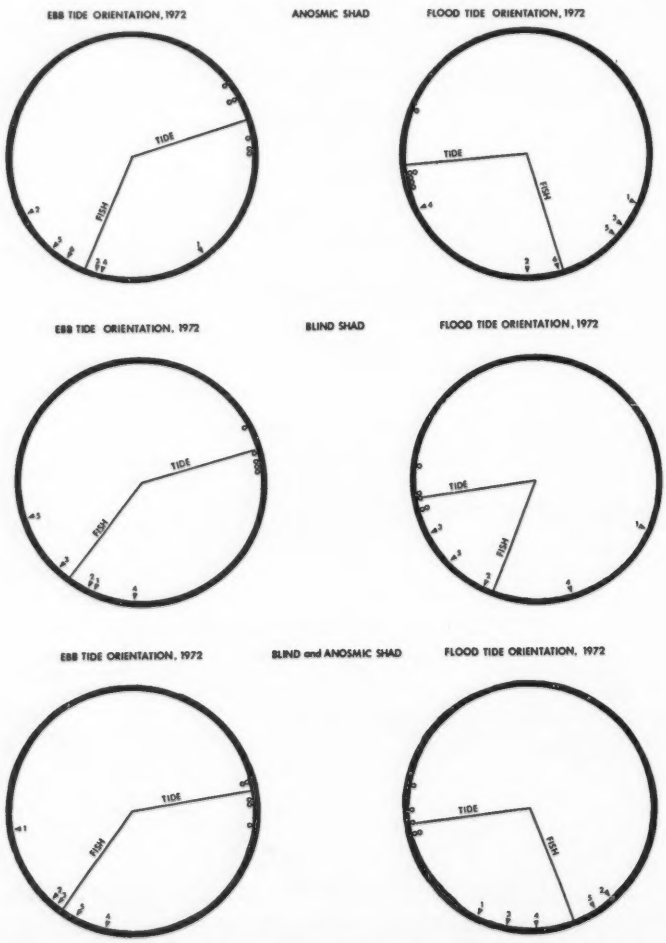

FIG. 5. Individual mean fish heading and tide direction for anosmic, blind, and blind/anosmic shad tracked in Long Island Sound in 1972.

TABLE 2. The frequency of large turning angles (>45°) calculated during ebb and flood tide conditions and pooled for each category of sensory-impaired shad tracked in Long Island Sound in 1972.

Fish treatment	Ebb tide		Flood tide		χ^2	P
	n turning angles	>45°	n turning angles	>45°		
Anosmic	111	57	94	42	0.32	>0.1
Blind	70	42	66	38	0.02	>0.1
Blind/anosmic	86	54	102	63	0.01	>0.1

frequency of large turning angles between ebb and flood tide conditions (Table 2). The frequencies of large turning angles exhibited by each impaired shad tracked in 1972 are presented in Table 3.

Response to Tidal Current Rate

The calculated swimming speeds of impaired shad, similarly based on 15-and 30-min time increments, were pooled within each category of sensory impairment and analyzed in relation to the rate of the ebb and flood tide currents. Anosmic shad swimming speeds were positively correlated with tidal current rate ($r = 0.24$, $n = 224$, $P<0.01$). This relationship was equally significant during daylight and darkness. Increases in current rate during the ebb tide produced greater increases in swimming speed ($b = 0.367$) than did similar increases in current velocity during the flood tides ($b=0.278$). No significant correlation was found between the calculated swimming speed of blind shad and tidal current rate ($r = -0.02$, $n = 148$, $P>0.1$). Calculated swimming speeds of blind/anosmic shad were positively correlated with tidal current velocities ($r = 0.201$, $n = 206$, $P<0.01$). This relationship was more significant during daylight ($r = 0.18$, $n = 128$, $P<0.05$) than darkness ($r = 0.14$, $n = 78$, $P>0.1$), but did not differ between ebb and flood tides.

Anosmic shad and blind shad swam at speeds greater than both tidal current rates. Blind/anosmic shad swam at speeds not significantly different from tidal current rates (Table 4).

The mean calculated swimming speeds of each sensory-impaired shad tracked during ebb and flood tide conditions in 1972 are presented in Table 5.

The observed swimming speeds of anosmic shad were positively correlated to surface salinities ($r = 0.24$, $n = 118$, $P<0.05$) but were not correlated to temperature. Neither blind shad nor blind/anosmic shad exhibited any significant correlation between observed swimming speed and surface salinity or temperature.

TABLE 3. The frequency of large turning angles (>45°) exhibited by each sensory-impaired shad during ebb and flood tide conditions.

Fish treatment	Fish no.	Release date	% large turning angles	
			Flood tide	Ebb tide
Anosmic	01	Apr. 25	16.6	85.7
	02	May 5	69.2	25.0
	03	May 7	36.8	33.3
	04	May 21	47.1	70.4
	05	May 24	42.9	66.7
	06	June 1	52.6	41.7
Blind	01	Apr. 27	62.5	50.0
	02	Apr. 29	33.3	60.0
	03	May 12	77.3	63.6
	04	May 23	50.0	57.1
	05	May 30	41.7	60.0
Blind/anosmic	01	May 2	50.0	42.8
	02	May 10	50.0	68.2
	03	May 18	71.4	72.7
	04	May 26	75.0	38.5
	05	June 3	66.7	69.7

Discussion

Unimpaired sonic-tagged shad tracked in Long Island Sound in 1970 and 1971 exhibited two major open water behavioral parameters; they tended to head into the reversing tidal current at all times and they altered their swimming speeds in relation to changes in tidal current velocities. This behavior, however, was not quantitatively equivalent during ebb and flood tide conditions. All unimpaired shad tracked in 1970 and 1971 headed into the ebb tide whereas during the flood tide, their orientation ranged from countercurrent to concurrent. This situation was reflected in the smaller frequency of

large turning angles exhibited by unimpaired shad during the ebb tide than during the flood tide. Increases in the rate of the ebbing tide resulted in greater increases in swimming speed than did similar increases in the rate of the flooding tide. This situation was reflected in the greater magnitude of swimming speeds while heading west during the ebb tide than during the flood tide. This combination of orientation and swimming behavior resulted in a net westerly displacement in Long Island Sound. Forty of 43 unimpaired shad tracked in 1970 and 1971 effected a net westerly movement during the ebb tide and either held their position or were slowly carried west by the flood tide (Dodson and Leggett 1973).

Anosmic and blind/anosmic sonic-tagged shad exhibited the same two major parameters characteristic of the behavior of unimpaired shad. This behavior, however, was equivalent during both tides. The pooled data for anosmic shad and for blind/anosmic shad revealed no differences in the frequency of large turning angles during ebb and flood tides. Furthermore, anosmic shad swam at speeds in excess of both tidal rates and blind/anosmic shad swam at speeds approximately equal to both tidal current rates. Therefore, anosmic and blind/

TABLE 4. Mean tidal rates and mean calculated swimming speeds of sensory-impaired sonic-tagged shad (pooled for each category of sensory impairment).

	Flood tide						Ebb tide					
		tidal rate (*cm/s*)		swimming speed (*cm/s*)		*t*-test		tidal rate (*cm/s*)		swimming speed (*cm/s*)		*t*-test
Fish treatment	*n*	mean	SD	mean	SD	*P*	*n*	mean	SD	mean	SD	*P*
Anosmic	98	53.6	26.5	76.5	33.5	<0.01	115	53.0	32.6	81.4	45.7	<0.01
Blind	70	50.3	28.9	74.1	54.9	<0.01	72	52.1	28.7	68.6	45.7	<0.02
Blind/anosmic	105	47.2	19.8	47.9	26.8	>0.05	89	53.9	26.8	61.6	36.6	>0.05

TABLE 5. Mean tidal rate and mean calculated swimming speed of individual sonic-tagged sensory-impaired shad tracked in Long Island Sound in 1972 during ebb and flood tide conditions.

		Flood tide				Ebb tide			
Fish treatment	No.	*n*	mean tidal rate (*cm/s*)	mean swim speed (*cm/s*)	*P*	*n*	mean tidal rate (*cm/s*)	mean swim speed (*cm/s*)	*P*
Anosmic	01	12	72.5	99.1	<0.05	8	82.9	75.6	>0.05
	02	16	59.1	85.7	<0.05	12	53.3	138.4	<0.01
	03	19	53.6	66.5	>0.05	19	58.8	74.4	>0.05
	04	17	34.1	73.8	<0.01	28	31.7	90.2	<0.01
	05	15	61.9	79.6	>0.05	12	74.7	90.2	>0.05
	06	19	47.2	64.9	>0.05	24	43.3	53.6	>0.05
Blind	01	7	55.8	48.8	>0.05	15	69.8	60.9	>0.05
	02	8	62.8	78.9	>0.05	5	56.1	66.5	>0.05
	03	24	55.5	73.8	>0.05	22	39.0	47.9	>0.05
	04	19	41.8	79.9	<0.01	15	65.2	78.9	>0.05
	05	12	42.4	73.2	<0.01	16	40.8	95.1	<0.01
B/A	01	12	43.6	42.4	>0.05	8	60.9	105.2	<0.02
	02	27	53.9	53.3	>0.05	22	64.3	42.4	<0.05
	03	7	43.9	72.9	<0.05	12	53.3	61.6	>0.05
	04	12	50.9	36.6	>0.05	14	53.6	85.3	<0.01
	05	47	43.6	45.1	>0.05	33	45.7	53.6	>0.05

anosmic shad failed to exhibit the westerly bias in behavior characteristic of unimpaired shad.

Analysis of the behavior of individual shad revealed that the apparent unbiased behavior of the anosmic group was the result of equal frequencies of westerly biased (anosmic shad 2 and 4), easterly biased (anosmic shad 1 and 3), and unbiased (anosmic shad 5 and 6) behavior. Four of five blind/anosmic shad exhibited no unidirectional bias in behavior. Only blind/anosmic shad 1 exhibited a westerly movement.

Blind shad failed to exhibit the tendency to head into the tidal current or the adjustment of swimming speeds relative to changes in tidal current velocity. The orientation of blind shad, however, was not equivalent during both tidal conditions. While tending to head into the ebb tide, blind shad exhibited concurrent and crosscurrent orientation during flood tide that resulted in a net westerly movement (blind shad 2, 3, and 5).

In an earlier paper (Dodson and Leggett, 1973) we proposed that two sets of environmental clues were used by shad in locating their home river. We distinguished between those clues used by shad to respond to changes in tidal current rate and direction and those responsible for establishing the westerly bias in behavior which resulted in movement from the Atlantic Ocean west toward the Connecticut River. The tracking of sensory-impaired shad in 1972 partially supports such a hypothesis. Deprivation of olfactory clues impaired shad's ability to maintain a consistent westerly bias and subsequent westerly displacement without eliminating the open water behavior patterns characteristic of the behavior of unimpaired shad. However, deprivation of visual clues impaired shad's ability to behave in a similar manner to unimpaired shad without eliminating their ability to maintain a westerly displacement in Long Island Sound.

The tracking of blind/anosmic sonic-tagged shad illustrated that the distinction between the roles of vision and olfaction in establishing the observed behavior is not clear. The fact that four of six anosmic shad exhibited some form of unidirectional bias in orientation whereas only one of five blind/anosmic shad did so suggests that visual clues may be involved in maintaining a directional bias. In addition, the observed ability of blind/anosmic shad to exhibit the 2 major parameters of behavior characteristic of unimpaired shad suggests that visual clues are not solely responsible for detection of changes in current rates and direction.

The tendency of anosmic shad to orient at right angles to the ebbing tide resulted in four of six anosmic shad migrating to the south shore of Long Island Sound. Only one unimpaired shad followed a similar path. In addition, few shad are caught along the south shore of Long Island Sound as no major tributaries are located there (Walburg and Nichols 1967). This southerly movement may have resulted from a search for olfactory clues indicative of the Connecticut River. The observed swimming speeds of anosmic shad decreased when surface salinities declined whereas unimpaired sonic-tagged shad increased their observed swimming speeds under similar conditions (Dodson and Leggett 1973). This behavior may have resulted from attempts by anosmic shad to search out olfactory clues normally associated with reduced salinities.

The net westerly movement of unimpaired shad tracked in 1970 and 1971 caused these fish to move west beyond the Connecticut River. The fact that both sonic-tagged and dart-tagged shad were subsequently recaptured in the Connecticut River indicates that this westerly bias was reversed at some point along the migration. Three unimpaired shad tracked in 1970 exhibited such a reversal resulting in easterly movement toward the Connecticut River. We proposed (Dodson and Leggett 1973) that the environmental clues responsible for establishing the initial westerly bias were also responsible for reversing the bias leading to movement toward the river once it had been passed. The reduced ability of blind/anosmic shad and anosmic shad to locate the home river, and the observed ability of blind shad to home from 10 km away without a significant reduction in success suggests that olfactory clues are instrumental in initiating the initial westerly bias and, subsequently, reversing this bias. The reduced homing ability of blind shad released at Saybrook is difficult to account for. Visual clues do not appear to become more important as the river is approached because blind shad homed successfully from Westbrook. Further work is required to identify the reasons for this result.

The observed differences between the behavior of sensory-intact shad tracked in 1970 and 1971 (Dodson and Leggett 1973) and sensory-impaired shad tracked in 1972 could have resulted from annual differences in environmental conditions and/or the motivational state of shad.

If the overall behavior of the annual population was affected by such factors we would expect the changes to be reflected in the timing of the shad run in the Connecticut River, and possibly also in the average rate of upriver migration.

Catch/effort data from an experimental gillnet fished daily at the mouth of the Connecticut River throughout the shad runs of 1970 to 1972 revealed that the date of the first shad capture varied by only 1 day and the date of the median shad capture

by only 4 days over the 3 yr. In addition the rate of upriver migration was similar, with the largest difference occurring between 1970 and 1971 when unimpaired fish were being tracked (1970 — 2.7 km/day; 1971 — 2.3 km/day; 1972 — 2.4 km/day; W. C. Leggett unpublished data). River discharge volumes during April and May varied during the period, but the differences were small (1970 — 47.6×10^3 cfs average; 1971 — 46.1×10^3 cfs average; 1972 — 53.1×10^3 cfs average). The greatest difference between the years occurred in population size (1970 — 730,000; 1971 — 705,000; 1972 — 397,000); however, these population fluctuations are known to have resulted from differences in recruitment and escapement (W. C. Leggett unpublished data) and do not appear to be influenced by environmental factors (Fredin 1954; W. C. Leggett unpublished data). In addition the frequency of recovery and mean homing times of unimpaired shad released in Long Island Sound in 1971 and 1972 did not differ significantly. While the possibility remains that behavioral changes could have occurred without altering the above population characteristics we feel a more tenable conclusion is that the observed differences in behavior of unimpaired and impaired shad resulted from sensory impairment.

It is also possible that sensory impairment may have caused differences in behavior that transcend the loss of the cue or sense. Peters (1971) noted the possibility that olfactory impairment may affect behavior patterns not directly associated with odor stimuli. However, removal of the olfactory bulbs has not resulted in deficits in reproductive behavior, parental activities, aggressive behavior, or schooling (Aronson 1970). In this study, sensory mutilation was avoided and shad were not held or displaced after the sensory occlusions, but were released immediately in an attempt to minimize possible traumatic effects and behavior modifications related to handling and occlusion.

The available data indicate that an olfactory–rheotaxic mechanism forms the basis of the non-random search pattern displayed by unimpaired Connecticut River shad in locating their home river. The westerly bias in the open water migration characteristic of unimpaired shad entering Long Island Sound appears to be most directly governed by olfactory clues emanating from the Connecticut River while the unidirectional displacement is governed by reference to the rate and direction of the tidal currents. Behavioral and electrophysiological studies have demonstrated the ability of fish to detect low concentrations of odor, and to discriminate one or more odors in a mixture. They have also implicated olfactory clues in the process of parent stream recognition (Kleerekoper 1969; Harden-Jones 1968; Hara 1970). However, to guide fish directly to their home river the concentration gradient of the odor must be sufficiently steep to elicit a klino or tropotaxis (Hara 1970). Such steep gradients do not exist in Long Island Sound where the strong reversing currents dilute and disperse home river clues both to the east and west of the Connecticut River. The historical and present abundance of shad west of the Connecticut River during spawning migrations (Walburg and Nichols 1967) and the observed westerly movement of shad already west of the Connecticut River supports this view.

The response by shad to changing water velocities and current directions is less clearly defined. Water currents may provide unambiguous directional clues to migrating fish but the sensory pathways involved in orientation is a point of considerable speculation. In this study visual clues were implicated but were clearly not solely responsible for the rheotaxis. Semicircular canals (Gray 1937), electromagnetic clues (Royce et al. 1969), and tactile clues (Harden-Jones 1969) have been suggested as possible alternatives to sight. No evidence exists to evaluate the ability of shad to utilize such cues.

The results of the present study lead us to the following hypothesis concerning the homing migration of American shad. The cyclical and precisely timed nature of their extensive oceanic migration (Leggett and Whitney 1972) brings both mature and immature shad into the vicinity of their home river and of the characteristic odors of the system once a year.

In the case of Connecticut River shad, Connecticut River water has been detected off Montauk Point (Riley, 1959) well within the proposed oceanic migration route of the species. At this point olfactory clues, indicative of the Connecticut River act as a positive reward in a conditioning process whereby shad moving to the west are rewarded by remaining within the detectable odor field, those moving to the east are not.

Immature shad are believed to migrate with the adults at sea (Talbot and Sykes 1958). Since immature shad do not join in the spawning migration, it is possible that the onset of sexual maturity is directly related to the perception and/or recognition of the olfactory stimulus. The hormonal state of the animal in relation to gonad development could operate to moderate this response.

Once the required westerly bias is established, reference to the tidal currents provides the necessary directional information and maintains the fish on an east–west axis. Once established, the westerly bias in behavior would continue until the river is reached or, as apparently happens in a great many instances, the shad move west beyond the river and

the limits of its odor plume. In the latter instance another reward-non-reward conditioning process may establish an easterly bias leading to movement in the direction of the river. This sequence of westerly and easterly movements may occur several times before the river is located. This would explain the relatively long homing times from distances as short as 10 km. Eventual recognition of the home river appears to involve both olfactory and visual clues.

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Fish-to-Fish Attraction and the Facilitation of Feeding Behavior as Mediated by Visual Stimuli in Striped Mullet, *Mugil cephalus*

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Single juvenile striped mullet, *Mugil cephalus*, tested in a specially designed experimental tank system, were allowed visual contact with a group of fish located in one of four adjacent tanks. Attraction of mullet isolates was greatest to a group of species mates, and less to bluefish, *Pomatomus saltatrix*, and Atlantic mackerel, *Scomber scombrus*, groups, respectively.

To study the role of visual stimuli in feeding behavior, responses of mullet isolates were measured under three different test conditions: 1) absence of a group of species mates, 2) presence of a feeding group, and 3) presence of a nonfeeding group. Isolates tested in the absence of a group began feeding only after some delay, although the total number of subsequent feeding responses remained high. When isolates viewed a feeding group, the initiation of feeding was greatly facilitated, with the total number of feedings remaining high until the latter part of a test. Isolates viewing a nonfeeding group showed inhibition in the latency to feed as well as a low number of grazing responses. The significance of these observed responses is discussed.

OLLA, B. L., AND C. SAMET. 1974. Fish-to-fish attraction and the facilitation of feeding behavior as mediated by visual stimuli in striped mullet, *Mugil cephalus*. J. Fish. Res. Board Can. 31: 1621–1630.

Des jeunes muges cabots, *Mugil cephalus*, soumis isolément à des essais dans un système de bassins expérimentaux spécialement construits, ont pu avoir un contact visuel avec un groupe de poissons placés dans un de quatre bassins adjacents. Le muge isolé est attiré le plus vers un groupe de ses congénères, et à un degré moindre vers des groupes de tassergals, *Pomatomus saltatrix*, et de maquereaux atlantique, *Scomber scombrus*, respectivement.

Afin d'étudier le rôle de stimuli visuels dans le comportement alimentaire, nous avons mesuré les réponses de muges isolés dans trois conditions expérimentales différentes: 1) absence d'un groupe de congénères, 2) présence d'un groupe en train de se nourrir et 3) présence d'un groupe qui ne mange pas. En l'absence d'un groupe, les muges commencent à se nourrir seulement après un certain délai, bien que le nombre total de réponses alimentaires demeure élevé. Lorsque les muges isolés voient un groupe en train de se nourrir, le début de l'alimentation est grandement facilité, et le nombre total de réponses se maintient à un niveau élevé jusque durant la dernière partie d'un essai. Les muges isolés qui voient un groupe qui ne se nourrit pas montrent une certaine inhibition dans le temps de réaction à se nourrir et ont un petit nombre de réponses alimentaires. Nous examinons la signification de ces réponses observées.

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THE mutual attraction among fish represents the fundamental component of school formation. While several sensory modalities may mediate the attraction, the dominant role played by vision has been established for many species (see Shaw 1970 for comprehensive review). One facet of basic fish-to-fish attraction involves visual stimuli that must be appropriate not only for initial aggregation, but also for support and enhancement of the coherent character and synchrony of the school. The visual signals critical to this phase of attraction most

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likely arise from an interaction between anatomical features and specific behavior patterns of schooling individuals.

Another facet of mutual attraction is the social interaction reflected in the positive facilitation of certain activities of the school, e.g. feeding or spawning. These activities may be at least in part mediated by visual cues arising from specific behavior patterns. The adaptive and selective advantage of schooling for feeding and spawning, as well as for protection and migration, has been discussed by Manteifel and Radakov (as cited by Shaw 1970).

Our aim in this work was to study 1) the fish-to-fish attraction of juvenile striped mullet, *Mugil cephalus*, as mediated solely by vision, and 2) the social facilitation of feeding responses by visual stimuli arising from the behavior of species mates.

Materials and Methods

The juvenile mullet, *Mugil cephalus*, bluefish, *Pomatomus saltatrix*, and Atlantic mackerel, *Scomber scombrus*, used in these experiments were captured by seine net in tide pools along Sandy Hook, N. J. Mullet ranged in length from 10.0 to 15.0 cm, bluefish from 10.8 to 15.0 cm, and Atlantic mackerel from 10.0 to 15.0 cm. Groups of 8–10 fish were maintained in 110–190-liter tanks, each filtered and aerated by subgravel filters. Water temperatures ranged from 18.0 to 21.0 C, salinity from 22 to 24‰, and pH was held at 7.7 ± 0.1 in both holding and experimental tanks. In the holding room, an overhead fluorescent lighting system was connected to a time clock set for a 12-h light period. A 7.5-W incandescent bulb provided a low-level night illumination. To each holding tank of mullet we introduced 1.0 g of Purina Trout Chow daily for maintenance feeding. During the course of the feeding experiments, the feeding regimen for test fish was altered as described below.

The experimental tank system consisted of a 200-liter central tank, 67 × 64 × 47 cm, constructed of nonreflective glass with the walls joined by a silicone-based sealing compound. Situated within 2 cm of each wall of the central tank was a single, smaller 150-liter tank, constructed of regular plate glass, 74 × 45 × 46 cm (Fig. 1). The four outer tanks were fitted with subgravel filters covered with a 4-cm layer of 2–5 mm aquarium gravel. The central tank contained an equivalent layer of gravel but had an external sand and gravel filtration system that operated only before and after each test period. A single fluorescent bulb suspended over each of the four outer tanks provided indirect illumination of 350–400 mc at the surface of the central tank.

Within the central tank was a removable, opaque fiberglass cylinder, 42 cm high and 24 cm in diameter. The cylinder, open at both ends, served as an isolation chamber (IC) for a single fish before it was tested. The cylinder could be raised or lowered by an electric motor with associated wires, pulleys, and a counterweight. At the start of each test the cylinder was raised, releasing the fish into the central tank. Suspended above this apparatus was a 94- × 94-cm mirror with a 33- × 33-cm opening in the center. As the cylinder rose at a rate of 10–12 cm/s, it passed through the opening and came to rest above the mirror, remaining there for the duration of the test. The observer sat behind a black curtain that surrounded the tanks and viewed the mirror through a 40- × 40-cm opening. Quantitative data were recorded on a two channel strip recorder. A tape recorder was used by the observer to supplement these observations.

Visual Attraction of Mullet Isolates to Group

To test the attraction of an isolate to species mates, a naive mullet (one not previously tested) was transferred from a holding tank into the IC in the central tank 60 min prior to a test. At the same time four mullet (to serve as the group) were introduced into one of the adjacent tanks with the location selected at random.

Four isolates were tested individually for two, 120-min periods (Test X and Y) separated by a 60-min rest period. At the start of the test, the IC was raised and the isolate released. Observations were made of the time taken (latency) for the isolate to reach the wall at which the group was located and for the 120-min test, the time the isolate spent responding to the group. Periodic observations were made on the group's behavior.

At the end of the 120-min test, the isolate was returned to the IC and held for 60 min. During this time, the group fish were moved to one of the other three adjacent tanks selected at random. Then the isolate was released to begin Test Y with observations made as in the previous test.

To test the attraction of juvenile mullet isolates to juvenile bluefish or mackerel, we exposed four naive mullet isolates individually to groups of either four juvenile bluefish or four juvenile mackerel. Each mullet was tested twice on the same day (Test X and Y) as described above. The location of the bluefish or mackerel group was changed after the first test.

Facilitation of Visually Mediated Feeding Responses

This series of experiments was conducted in the same experimental apparatus as described above. Feeding responses of mullet isolates were measured in three different test situations: 1) the absence of any group; 2) the presence of a group of mullet feeding in an adjacent tank; and 3) the presence of a nonfeeding mullet group in an adjacent tank. Holding conditions were the same as described above with the exception of the fish that were to be used as isolates. These were held in tanks with 8 or 9 mullet, none of which was fed for 4 days preceding a test. During a test, liquified Purina Trout Chow, contained in a polyethylene bottle outside the viewing curtain, was introduced into the central tank via glass tubing. Hand pressure on the bottle released approximately 1.0 g of food into the tank at the appropriate time.

Five naive isolates were used for each series of tests. In each instance, the isolate was held for 60 min in the IC prior to the start of a test. Following each test, the central tank was drained and the top layer of gravel removed to eliminate any remaining food. Adjacent tanks were similarly treated prior to tests using nonfeeding fish.

Isolate feeding in the absence of a group — After a holding period of 60 min in the IC, the isolate was released into the tank. Food was introduced 15 min later and observations made of the time taken (latency) until the initial feeding and number of feeding bouts (any occurrence of grazing) during the next 60 min.

Isolate feeding in the presence of a feeding group — While the isolate was held in the IC for 60 min prior to the test, a group of four mullet was introduced into one of the adjacent tanks chosen at random. Food was introduced to the group 10 min before the isolate was released from the IC, thereby insuring that the group would be feeding at the onset of the tests. After release, the isolate was observed for 15 min before food was introduced into the central tank. Observations, as described above, were made for the next 60 min.

Isolate feeding in the presence of a nonfeeding group — During the 60-min period in which the isolate was held in the IC, a group of four nonfeeding mullet was

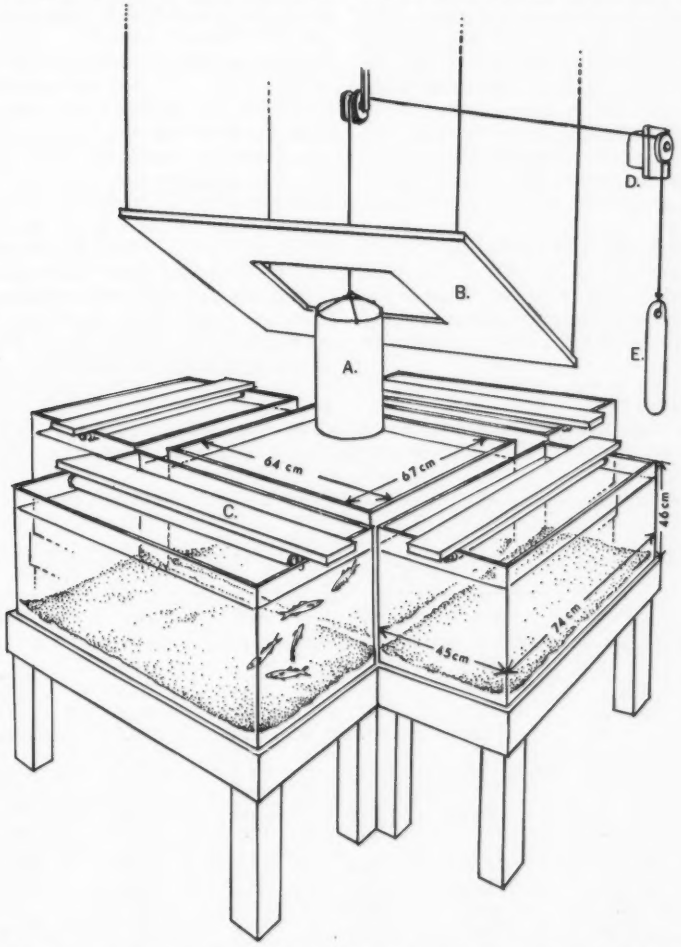

FIG. 1. Testing apparatus consisting of a central tank with four adjacent tanks. A, isolation cylinder; B, mirror; C, fluorescent lights; D, motor (to raise cylinder); E, counter weight.

placed in a randomly chosen adjacent tank. Food was introduced into the central tank 15 min after the isolate was released from the IC. Observations on behavior and feeding continued for the next 60 min.

Results

Attraction of Mullet Isolates to Groups

When the isolation chamber (IC) was raised to begin a test, mullet isolates generally skulled with the pectoral fins in the release area or swam around the tank. Then, once perceiving the group, the isolates responded in either of two ways. In one case, the fish swam to the wall exposing the group and made contact with the snout or other cephalic portions, swimming back and forth along the length of the wall or swimming in place against the wall. In the second type of response the isolates faced the group and skulled the water remaining within 5.0 cm of the wall such that visual perception of the group was presumably occurring. Both responses at the group wall were considered indicative of attraction.

During the course of a test the isolate would at times move randomly from the wall at which the group was located to other walls. When not at the group wall, the isolate was always in close proximity to one of the walls of the tank, never remaining in the center.

Isolates exposed to mullet groups — The mullet group generally aggregated in a particular location in their tank, but the specific activities of the group were not always synchronized. The group was usually located in the central front area of their tank (i.e. the area directly adjacent to the isolates' tank). Some group fish actively swam or slowly skulled the water, turning in different directions, while others vigorously contacted the front wall, apparently responding with mutual visual attraction to the mullet isolate. At times the group appeared not to respond to the isolate, aggregating either toward the back or on one side of their tank. Some of the group would skull while others would swim slowly or contact the wall.

After the IC was raised, isolates took from 3.6 to 36.3 s ($\bar{x}$ = 11.0 s) to reach the group wall. There was no significant difference in the latency to reach the group wall between first and second tests ($P>0.05$, substitute t-test; Lord 1947).

It was apparent that there was a strong visual attraction of mullet isolates to species mates in an adjacent tank. Isolates spent 88.1–97.8% of the combined total test time of 240 min at the tank wall at which the group was exposed (Table 1). During the course of each exposure, the isolates' attraction to the group significantly declined after the first 60 min in both the X and Y tests ($P \leq 0.01$; Yates Algorithm with levels of significance for

Table 1. Duration of attraction of isolates exposed to groups of mullet (*Mugil cephalus*), bluefish (*Pomatomus saltatrix*), and Atlantic mackerel (*Scomber scombrus*) expressed in minutes and as percentages of total combined test time.

Exposure of isolates to	Isolate	Test X		Test Y		Total Test X + Test Y	
		min	%[a]	min	%[a]	min	%[b]
Mullet groups	1	108.0	90.0	103.4	86.2	211.4	88.1
	2	114.0	95.0	113.8	94.8	227.8	94.9
	3	100.9	84.1	114.7	95.6	215.6	89.8
	4	117.0	97.5	117.7	98.1	234.7	97.8
Bluefish groups	5	117.2	97.7	80.4	67.0	197.6	82.3
	6	117.4	97.8	42.0	35.0	159.4	66.4
	7	92.9	77.4	106.3	88.6	199.2	83.0
	8	86.7	72.4	74.1	61.8	161.0	67.1
Mackerel groups	9	66.8	55.7	39.4	32.8	106.2	44.3
	10	72.1	60.1	66.7	55.6	138.8	57.8
	11	40.7	33.9	48.5	40.4	89.2	37.2
	12	94.6	78.8	71.8	59.8	166.4	69.3

[a]Response time as percentage of single 120-min test.
[b]Response time as percentage of two 120-min tests.

effects determined by a *t*-test; Table 2). However, the 60-min rest period between the first 120-min test (Test X) and the second (Test Y) served to reestablish the level of attraction with the result that there were no significant differences in the attraction between Test X and Y (Table 2).

We performed two preliminary experiments to examine the persistence of the response beyond the normal testing procedure of two 120-min tests. In one case we retested an isolate (No. 4) for an additional 120-min period, 60 min after Test Y. On this third exposure of the isolate to the group, the fish spent 90.8% of the total test time at the group wall. This was only a slight decrease from the previous two tests.

In another experiment, we exposed a naive fish to a mullet group continuously for 24 h in constant light while observing the behavior of the fish for 10 min each hour. During the first 16 h this isolate exhibited a high level of attraction to the group, and while the response was not always consistent, it was within the normal range of behavioral variability we had observed during previous exposures (i.e. during the first, second, third, or fourth 60-min periods). Following 16 h of exposure, the response of the isolate began to wane below that observed in previous experiments, being completely extinguished by 22 h, when the isolate remained exclusively at a nongroup wall. During this latter period the isolate slowly skulled the water, a possible indication of fatigue. This was a distinct change from the vigorous contact activity observed during its earlier response to the group.

It was apparent from these results that vision played an important role in the fish-to-fish attraction of mullet. All the isolates tested showed a high degree of attraction to mullet groups, with the response persisting for long periods.

Isolates exposed to bluefish groups — The only difference in group behavior of the bluefish, compared to the mullet, was the higher degree of syn-

TABLE 2. Duration of attraction of mullet isolates to mullet groups as measured by the number of minutes at the group wall in a 15-min period. All averages and differences are on this scale.

15-min periods	Isolate 1	Isolate 2	Isolate 3	Isolate 4	Minutes 15 Avg	15 Diff.	30 Avg	30 Diff.	60 Avg	60 Diff.	120 Avg	120 Diff.
					Test X							
1	15.00	14.63	15.00	15.00	14.91							
2	13.58	14.07	15.00	14.97	14.40	−0.51	14.65					
3	12.80	14.95	14.95	14.75	14.36							
4	14.17	13.05	14.92	14.22	14.09	−0.27	14.22	−0.43	14.44			
5	13.43	14.95	13.85	14.40	14.15							
6	12.78	14.53	8.82	14.62	12.69	−1.46	13.42					
7	12.60	13.42	10.02	14.73	12.69							
8	13.70	14.43	8.10	14.30	12.63	−0.06	12.66	−0.76	13.04	−1.40	13.74	
					Test Y							
9	15.00	14.52	13.82	14.93	14.57							
10	14.82	14.73	14.92	14.32	14.69	+0.12	14.63					
11	14.95	14.10	15.00	14.58	14.66							
12	13.80	14.62	14.52	14.73	14.42	−0.24	14.54	−0.09	14.58			
13	13.25	14.23	15.00	14.90	14.34							
14	12.17	14.10	14.93	14.90	14.02	−0.32	14.18					
15	6.15	12.88	12.23	14.82	11.52							
16	13.27	14.65	14.33	14.58	14.21	+2.69	12.86	−1.32	13.52	−1.06	14.05	+0.31
Avg effect[a]					A = −0.01		B = −0.65		C = −1.23		D = +0.31	
Probability					>0.05		>0.05		≤0.01		>0.05	

[a]A is the average difference in response between even-and odd-numbered periods and represents the effect of 15-min exposure to the group. B represents the effect of 30-min exposure, C the effect of 60-min exposure, and D the effect of 120-min exposure with 60-min rest between tests.

chronization of the movements among bluefish. As with the mullet, the bluefish generally skulled slowly as a cohesive group in the center of the tank, facing the isolates' tank at a distance of 10–20 cm. Occasionally the bluefish also responded directly to the isolate with vigorous contact behavior at their mutual wall.

When the IC was raised to begin a test, isolates took from 2.5 to 9.6 s ($\bar{x}$ = 6.0 s) to reach the wall at which the bluefish group was located. There was no significant difference ($P>0.05$, substitute *t*-test) between latencies in Test X and Y for each fish.

The overall duration of the visual attraction to the bluefish was somewhat less than that to mullet. Mullet isolates spent from 66.4 to 83.0% of the combined test time at the group wall (Table 1). The lower level of responsiveness to bluefish groups was most evident during Y Tests (second tests), when there was a significant decrement in attraction ($P\leq0.01$, Table 3). The 60-min rest period between 120-min tests did not serve to maintain or reestablish the response level as it did with mullet groups. Isolates became less attracted to the bluefish groups with time.

Isolates exposed to Atlantic mackerel groups — The mackerel group behavior was quite different from that of either the mullet or bluefish groups with the mackerel constantly swimming and synchronizing the direction of their movements. The fish moved as a cohesive school, either swimming in a complete circuit around their tank or back and forth along the length of the walls. The mackerel often contacted the walls with the sides of their bodies. As they moved along the front wall at which the isolate could be seen, cephalic-snout contact was often made.

Mullet isolates, when released from the IC, took from 2.9 to 11.8 s ($\bar{x}$ = 7.2 s) to reach the group wall. There was no significant difference in latencies between X and Y Tests ($P>0.05$, substitute *t*-test).

The attraction of mullet isolates to Atlantic mackerel was decidedly less than either to mullet or bluefish groups. In the combined test time of 240 min, isolates spent 37.2–69.3% at the group

TABLE 3. Duration of attraction of mullet isolates to bluefish groups as measured by the number of minutes at the group wall in a 15-min period. All averages and differences are on this scale.

15-min periods	Isolate 5	6	7	8	Minutes 15 Avg	15 Diff.	30 Avg	30 Diff.	60 Avg	60 Diff.	120 Avg	120 Diff.
					Test X							
1	14.20	14.93	7.38	13.83	12.59							
2	14.80	14.98	5.40	14.42	12.40	−0.19	12.50					
3	14.73	14.92	14.73	13.60	14.50							
4	14.60	14.93	14.53	11.22	13.82	−0.68	14.16	+1.66	13.33			
5	14.80	14.92	13.02	6.87	12.40							
6	14.92	14.88	10.13	5.80	11.43	−0.97	11.92					
7	14.78	14.78	14.58	9.02	13.29							
8	14.35	13.37	13.15	12.15	13.26	−0.03	13.28	+1.36	12.60	−0.73	12.97	
					Test Y							
9	12.37	8.61	8.50	14.73	11.05							
10	7.52	4.88	9.32	7.85	7.39	−3.66	9.22					
11	14.53	5.77	14.83	8.33	10.87							
12	3.57	6.28	14.88	10.87	8.90	−1.97	9.89	+0.67	9.56			
13	9.65	5.43	14.92	7.72	9.43							
14	12.03	3.43	14.57	7.53	9.39	−0.04	9.41					
15	14.02	4.38	14.87	8.17	10.36							
16	6.67	3.23	14.47	8.95	8.33	−2.03	9.35	−0.06	9.38	−0.18	9.47	−3.50
Avg effect[a]					A = −1.20		B = +0.91		C = −0.46		D = −3.50	
Probability					>0.05		>0.05		>0.05		≤0.01	

[a]See Table 2 footnote.

wall (Table 1). There was a significant decrease in attraction between the first and second 60 min of each 120-min test ($P \leq 0.05$, Table 4). Following the 60-min rest period after Test X, the response to the mackerel was reestablished in Test Y, but was again indicative of a low level of attraction as in Test X.

Despite a high level of fish-to-fish variation in attraction, it was obvious that intraspecific responses were strongest and most persistent. While the isolates were attracted equally to bluefish and mullet groups during the X Tests ($P > 0.05$, substitute *t*-test), by the Y Tests the degree of attraction to bluefish groups had significantly waned ($P \leq 0.05$). Attraction of isolates to mackerel groups was less than that to mullet groups in both X and Y Tests ($P \leq 0.01$).

Feeding Behavior of Mullet

From our laboratory observations on groups of 8–10 mullet feeding, it was evident that when food was introduced, the organized patterns of parallel orientation and directional swimming as a schooling unit gradually diminished. As the fish began to graze, they would tilt head down towards the sand, ingesting particles of sand and food (feeding behavior essentially the same as described by Odum 1970). The fish tended to remain grouped, feeding together in the same general area although food was dispersed across the bottom of the tank. At times, four to six fish would graze together with their snouts within several centimeters. Frequently during these feeding bouts, the flanks of several mullet would touch for up to 3–4 s. It was apparent that there was a strong social interaction between fish during feeding.

Based on these observations and our findings of visual fish-to-fish attraction, we performed a series of experiments to examine the role that visually mediated social stimuli play in facilitating feeding responses. Test subjects consisted of mullet isolates with feeding responses measured under the three different test conditions described previously.

Table 4. Duration of attraction of mullet isolates to mackerel groups as measured by the number of minutes at the group wall in a 15-min period. All averages and differences are on this scale.

15-min periods	Isolate 9	10	11	12	Minutes 15 Avg	15 Diff.	30 Avg	30 Diff.	60 Avg	60 Diff.	120 Avg	120 Diff.
					Test X							
1	14.87	8.85	11.40	15.00	12.53							
2	14.10	12.65	4.02	14.88	11.41	−1.12	11.97					
3	7.67	12.01	2.82	14.40	9.23							
4	7.28	10.05	3.48	11.72	8.13	−1.10	8.68	−3.29	10.33			
5	9.87	7.62	3.93	5.73	6.79							
6	3.52	7.57	5.75	9.58	6.61	−0.18	6.70					
7	5.72	6.53	3.77	9.62	6.41							
8	3.83	6.82	5.53	13.65	7.46	+1.05	6.94	+0.24	6.82	−3.51	8.58	
					Test Y							
9	7.97	7.37	11.12	10.68	9.29							
10	5.20	7.77	4.77	5.83	5.89	−3.40	7.59					
11	3.67	8.67	5.20	5.65	5.80							
12	5.28	12.12	4.92	5.20	6.88	+1.08	6.34	−1.25	6.97			
13	5.68	12.20	5.47	7.08	7.61							
14	5.17	6.22	5.40	8.40	6.30	−1.31	6.96					
15	4.20	7.03	7.00	14.88	8.28							
16	2.50	5.37	4.60	14.10	6.64	−1.64	7.46	+0.50	7.21	+0.24	7.09	−1.49
Avg effect[a]					A = −0.83		B = −0.95		C = −1.63		D = −1.49	
Probability					>0.05		>0.05		≤0.05		>0.05	

[a]See Table 2 footnote.

TABLE 5. Responses (number of feeding bouts per 15-min period) of mullet isolates tested: a) in the absence of a group, b) in the presence of a feeding group, and c) in the presence of a nonfeeding group.

Test	Absence of a group							Feeding group							Nonfeeding group						
	Isolate							Isolate							Isolate						
15-min periods	1	2	3	4	5	R_5	$\bar{x}_5$	6	7	8	9	10	R_5	$\bar{x}_5$	11	12	13	14	15	R_5	$\bar{x}_5$
1	0	35	12	20	26	35	18.6	37	15	12	28	9	28	20.2	0	0	0	0	0	0	0
2	21	40	26	37	29	19	30.6	22	6	6	38	29	32	20.2	1	1	0	0	2	2	0.8
3	17	34	41	24	15	26	26.2	48	8	5	24	16	43	20.2	2	3	1	3	2	2	2.2
4	17	35	29	19	23	18	24.6	6	1	3	15	1	14	5.2	3	1	2	0	2	3	1.6
Σ 60	55	144	108	100	93	89	100	113	30	26	105	55	87	65.8	6	5	3	3	6	3	4.6

Isolates feeding with no group present — Our aim was to measure the feeding response of an isolate in the absence of any visual stimulation from species mates in an adjacent tank. For the 15-min period after the IC was raised and before food was introduced, isolates swam around the perimeter of the tank, contacting the four walls.

After food was introduced, an isolate began to feed after a latency ranging from 5.39 to 16.87 min ($\bar{x}$ = 8.66 min). Each isolate grazed in short bouts across the bottom of the tank, with each bout lasting from 1.3 to 3.0 s. The total feeding bouts per fish ranged from 55 to 144, indicating fish-to-fish differences but no significant difference with time ($P>0.05$, substitute *t*-test; Lord 1947; Table 5). This would indicate that feeding motivation remained substantially unchanged throughout the 60-min test period.

Isolates exposed to feeding group — After the IC was raised, isolates moved to the wall exposing the feeding group and remained there for the total 15-min period preceding food introduction. During this period, isolates did not graze.

Following introduction of food into the isolates' tank, feeding in the five tests began in 0.29–2.13 min ($\bar{x}$ = 1.23 min). Feeding initiation took significantly less time than in the absence of a group ($P\leq0.01$). Feeding bouts lasted 0.7–3.5 s and always occurred in front of the wall exposing the group even though food was dispersed across the bottom of the tank.

Total feeding bouts per fish ranged from 26 to 113 (Table 5). The mean number of feeding bouts decreased significantly during the last 15-min period of the five tests ($P\leq0.05$; Table 5). In contrast, feeding in the absence of a group did not diminish with time.

Isolates exposed to nonfeeding group — When the IC was raised, isolates moved to and remained at the wall exposing the nonfeeding group of mullet for the total 15-min period preceding food introduction. No feeding bouts were exhibited by isolates during this period.

Following food introduction, latencies to the initial feeding for the five tests ranged from 18.02 to 32.07 min ($\bar{x}$ = 24.21 min), significantly longer than for fish exposed to either a feeding group or to no group ($P\leq0.01$). During this period the isolates remained at the group wall vigorously bumping against it.

When grazing did begin, feeding bouts ranged from 1.2 to 3.1 s. The total number of feeding bouts remained significantly less than for fish exposed either to no group or a feeding group ($P\leq0.01$; Table 5), with six the largest number of bouts by any isolate during a 60-min test.

When isolates did feed, it was always in front of the wall exposing the group. As an isolate fed, it would break contact with the wall and move head down towards the sand facing the group.

Discussion

The results from the visual attraction experiments indicated that there was a high level of fish-to-fish attraction for mullet, mediated solely by visual cues. Using the definition of a school as "... an aggregation formed when one fish reacts to one or more other fish by staying near them" (Keenleyside 1955), it was evident that the intraspecific attraction of mullet could be considered as reflecting one major facet of the schooling reaction.

Intraspecific approach and attraction responses based solely on visual stimuli have been reported for the grey mullet, *Mugil chelo*; the roach, *Rutilus*

rutilus; the pomacentrid, *Chromis chromis* (Hemmings 1966), and for other species including sea catfish, *Plotosus anguillaris* (Sato 1938); threespine stickleback, *Gasterosteus aculeatus*; roach, *Leuciscus rutilus*; rudd, *Scardinius erythrophthalmus* (Keenleyside 1955); and *Menidia menidia* and *M. beryllina* (Shaw 1960). (For review and discussion see Morrow 1948; Atz 1953; Breder 1959; and Shaw 1970.)

The visual cues arising from the group activity and acting to attract isolates involve a combination of behavioral and anatomical features. The fact that mullet isolates, while being attracted to species mates, were also attracted, although to a lesser degree, to bluefish and Atlantic mackerel groups, indicates some generalization of the grouping response. Cues originating from all three species overlap more for mullet and bluefish. Interspecific attraction of single fish, allowed only visual contact with groups of different species, has been observed in rudd, *Scardinius erythrophthalmus*, and the characid, *Pristella riddlei* (Keenleyside 1955).

The level of attraction of mullet isolates for a mullet group reflects the specificity of responsiveness. If experiments were performed on closely related mullet species, it is possible that the anatomical and behavioral overlap would be such that no difference in interspecific attraction could be detected.

It is possible that the attraction of isolates to groups of other fish may have been, in part, reinforced by contact with the walls of the test tank. During each test, the isola es either "nosed" a small area of the glass wall or moved laterally along the wall at which the group was present. In holding tanks, mullet often make contact with one another during swimming and feeding. The contact with the wall may have provided a partial or surrogate fulfillment of the normal tactile response among species mates and played a role in sustaining the grouping response.

Bluefish are a natural predator of mullet. We have often observed, in nature, juvenile mullet jumping to escape predation from juvenile bluefish schools. During the present experiments, mullet never exhibited behaviors to the bluefish that could be considered as fright or avoidance activities.

The motivation to group by isolates may be at a higher level than that of avoiding predators on a purely visual basis, whereas in the natural environment, mullet may rely upon additional recognition signals for discriminating and avoiding potential predatory species.

The short latency to feeding initiation in isolates presented with food after viewing a feeding group indicated that the visual stimulus of other fish feeding resulted in the facilitation of the response in the isolate. Studies by Welty (1934) showed that social facilitation, reflected by a higher food consumption, occurred among fish in groups as compared with isolates.

The presence of a group, feeding or not, served to orient the feeding activities of an isolate towards the group, with isolates always grazing in close proximity and facing the wall at which the group was exposed. In a study that involved visual feeding cues with threespine stickleback, *Gasterosteus aculeatus*, the fish, while hungry, were more attracted by the sight of a feeding fish than either by fish not feeding or by food alone (Keenleyside 1955). Mullet isolates, when presented with food in the absence of a group, fed throughout the tank.

When an isolate was presented food, after and while viewing a nonfeeding group, feeding was inhibited as reflected by the long latencies to initiate feeding and the significantly smaller number of feeding bouts. The group in this case was apparently providing visual cues related to and stimulating group formation with the result that feeding motivation was subordinated.

Initiation of feeding was faster in isolates viewing a group that was feeding than when no group was present. However, the feeding response was stronger in the absence of a group, persisting at a high level for the duration of a test. The nonfeeding group probably provided visual cues stimulating group formation. Even though food was present and the isolates hungry, grouping became the priority drive as intake of food acted to lower the intensity of the feeding drive.

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Reproductive Potential of Two Lake Whitefish (*Coregonus clupeaformis*) Populations[1]

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The reproductive potential of two lake whitefish (*Coregonus clupeaformis*) populations with dissimilar growth rates was studied and compared. The smaller-sized Pigeon Lake females and the larger-sized Buck Lake females had similar ratios of gonad weight to body weight during the gonad development period, but the Pigeon Lake fish produced fewer but larger eggs. Spawning occurred in both lakes for a period approaching 4 mo in both open water and under ice cover in a wide range of water temperatures. Concentrated spawning occurred in shallow water over a boulder, gravel, and sand surficial lake sediment of both lakes. The incubation of whitefish eggs was retarded under ice cover but accelerated to hatching as the water warmed and the ice left the lakes in the spring. The length of the egg incubation period, not the size of the egg under incubation, governed the size of the hatching lake whitefish.

BIDGOOD, B. F. 1974. Reproductive potential of two lake whitefish (*Coregonus clupeaformis*) populations. J. Fish. Res. Board Can. 31: 1631–1639.

Nous comparons le potentiel reproducteur de deux populations de grands corégones (*Coregonus clupeaformis*) dont le rythme de croissance est différent. Les femelles du lac Pigeon, plus petites, et celles du lac Buck, plus grandes, ont des rapports poids des gonades-poids corporel semblables pendant la période de développement des gonades, mais les poissons du lac Pigeon produisent un nombre moindre d'oeufs qui sont par contre plus gros. La fraie se produit dans les deux lacs sur une période de près de 4 mois, aussi bien en eau libre que sous une couverture de glace, sur une gamme étendue de températures. Il y a concentration de la fraie en eau peu profonde, au-dessus de sédiments de galets, gravier et sable de la zone des brisants dans les deux lacs. L'incubation des oeufs est plus lente sous la glace, mais s'accélère jusqu'à l'éclosion avec le réchauffement de l'eau et la disparition de la glace des lacs au printemps. La taille à l'éclosion dépend de la durée de la période d'incubation, non de la grosseur de l'oeuf sous incubation.

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PIGEON and Buck lakes contain lake whitefish, *Coregonus clupeaformis*, populations with dissimilar growth rates. The growth rate of individuals in the Pigeon Lake population has declined over the past 18 yr, whereas whitefish in Buck Lake have maintained a similar growth pattern over the same period of time. The decline in the growth rate of the Pigeon Lake population was attributed to a reduction in the numbers of predators of lake whitefish and other competitive feeding forage fish from this ecosystem. In spite of the different growth rates noted between the two populations, the majority (97%) of lake whitefish from both populations with four completed annuli mature and spawn (Bidgood 1972).

Information on recruitment in lake whitefish populations is limited. Hart (1930) described the spawning and early life history of lake whitefish in Lake Ontario, near the southern boundary of the distribution of the species (Lindsey et al. 1970). Price (1940) experimentally compared the incubation period to hatching of lake whitefish eggs when subjected to different water temperature regimes.

Comparative studies on the reproductive potential of two populations of the same species of fish with documented dissimilar growth rates present a new approach to observations on reproduction. This paper describes and compares the maturation,

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fecundity, spawning, and egg incubation period in and size of young-of-the-year fish hatching from eggs from these two populations of lake whitefish.

Materials and Methods

Lake whitefish samples for gonad development studies were collected twice a month from January to March and from May to October, 1970 with gillnets set in Pigeon and Buck lakes. Buck Lake samples were collected 1 wk ahead of the sampling in Pigeon Lake in all cases. Vertical water temperature data were collected at 0.3-m intervals at each gillnet set. Scales were removed between the left lateral line and dorsal fin for age determination and the total weight of the fish and the weight of both gonads was recorded for each female captured (about 4000). Data from fish with atypical gonad development or a single gonad were discarded and only mature, female lake whitefish with four or more completed annuli (Bidgood 1973) were included in the analyzed samples.

Areas of spawning were documented with gillnet sets during the open water spawning period (October–November). The presence of ripe and spent male and female whitefish in the same gillnet sets, the absence of immature fish in the gillnet sets, the presence of tubercles, and the occurrence of nuptial displays (Hart 1930) on the surface at night indicated the areas of concentrated spawning. The duration of spawning in Pigeon and Buck lakes was determined by setting gillnets on the known spawning beds in the open water and through ice cover from mid-September to the end of January. Water temperatures were recorded at each gillnet set on the spawning beds. Spawning was designated as taking place when running ripe and spent female fish occurred together in these gillnet samples of about 3000 fish. Attempts to collect eggs on the boulder, rubble, and sand substrate by scuba diving in open water was not successful and therefore was not attempted under ice cover.

Fecundity was determined by weighing a sample of 50 eggs from the anterior, mid-, and posterior portion of the left gonad of 30 ripe fish from each lake. The mean weight of egg samples from each population was used to estimate the number of eggs in the weighed gonads of 60 mature fish from each lake. The oviduct egg (Fisher 1963) size of lake whitefish was measured as the average size of a sample of 50 eggs (Higham and Nicholson 1962) from the anterior, mid-, and posterior portion of the ripe ovary. Average egg size was calculated for each of the 30 samples from each of the three locations of the gonads.

Eggs from ripe lake whitefish captured in gillnets in the latter part of October, 1970 and 1971 were stripped, fertilized, and hardened in the appropriate water in jars. The jars were packed in ice and transported to the laboratory in 1½ h and placed under experimentation. Hardened eggs from both lake whitefish populations were incubated in three 213-cm × 61-cm × 60-cm rectangular fiberglass insulated Living Stream[2] recirculation troughs with an activated charcoal and an open pore foam rubber filter. Trough water temperatures were maintained at ±0.04 C of the desired temperature.

In 1970, eggs from both lake whitefish populations, stripped, fertilized, and hardened in Pigeon Lake and in Buck Lake water, were incubated in both segregated trays and closed system jar culture (Bidgood 1972) where the eggs were rolled and placed in two troughs containing Pigeon Lake water and one trough containing Buck Lake water. All eggs were incubated in darkness and exposed to daylight only for observations. The water temperature of one trough was controlled at 2 C for the duration of the experiment, a second trough was controlled at 4 C for the duration of the experiment, and a third trough was controlled at 2 C to the eyed-egg stage, raised to 4 C, and maintained at that water temperature for the duration of the experiment. Eggs were observed daily and the stage of development and number hatching in each of the three troughs was recorded. In 1971, the eggs from both lake whitefish populations were spawned, fertilized, hardened, and incubated on trays in Pigeon Lake water. The water temperature of one trough was controlled to 2 C for the duration of the experiment while the Pigeon and Buck Lake eggs in a second trough were incubated at 2 C for 70 and 76 days, respectively; then the incubating water temperature was raised at the rate of 0.5 C/week to 4.0 C to prevent thermal shock to the eggs that could cause an increase in egg mortality and maintained at that temperature for the duration of the experiment. The eggs in the trays were treated with a concentration of 1 g of refined Malachite green (1:200,000) for ½ h each week until the eggs eyed to control white spot disease (Wolf 1970). The number of fish hatching daily was recorded.

The average diameter of Pigeon and Buck Lake hardened and eyed eggs was measured as the mean size of samples of 50 eggs from each population. The total length of 30 whitefish from Buck Lake, measured on the day of hatching, was compared to that of 30 whitefish that hatched from Pigeon Lake eggs after both had incubated at 2 C for the same number of days. Further description of the methods are presented by Bidgood (1972). Student's *t*-test for unpaired observations and unequal variances was used in the statistical comparison of any two means of samples with equal observations.

Maturation

After the ice left Buck Lake on May 1 and Pigeon Lake on May 7, 1970, the gonad weight of mature (IV+ and older) female lake whitefish of both populations increased significantly (.01) every 2 wk under both a rising and falling spring, summer, and fall water temperature regime (Fig. 1). The Pigeon Lake population had similar ratios of gonad weight to body weight as those of the Buck Lake population when compared from breakup to the onset of spawning (October) since the slopes of the

[2]S. S. Filtration and Development Co. Ltd., Oakville, Ont.

two regression lines did not differ statistically ($P>0.05$) and were both estimates of the same line. No increase in gonad weight was evident in either population sampled under ice cover from January to April, 1970 when these fish were subjected to a cold, bottom water temperature regime that varied with depth of water and time of year from 0.7 to 1.7 C in Pigeon Lake and from 2.8 to 3.9 C in Buck Lake.

Fecundity

The fecundity of the Pigeon Lake lake whitefish population was lower than that of the Buck Lake population (Fig. 2). The number of eggs produced by the slower growing Pigeon Lake population was less variable than that of the faster growing Buck Lake population. The deviations of the fecundity of individuals in the Pigeon Lake sample from the calculated regression line ($r=0.66$) were less than that of the Buck Lake sample ($r=0.60$). The increase in the number of eggs produced with the increase in size of the females was greater in the Buck Lake sample than that of the Pigeon Lake sample of 60 female fish, since the slope of the regression line of the Buck Lake sample (4.03) was highly significantly greater ($P<0.0001$) than the slope of the Pigeon Lake sample (1.04). Pigeon Lake whitefish produced an average of 18,010 eggs/kg body weight or about 11,112 eggs/fish. Buck Lake females produced an average of 27,670 eggs/kg body weight or about 49,114 eggs/fish.

Oviduct eggs of Pigeon Lake females were larger than those of Buck Lake females. Pigeon Lake mean oviduct eggs varied from 1.86 mm in diameter in 1969 to 1.87 mm in 1970. Both means were significantly larger (.01) than the Buck Lake mean oviduct egg size of 1.77 mm in 1970. All eggs in the gonads of both populations matured at the same rate and ripened at the same time since no

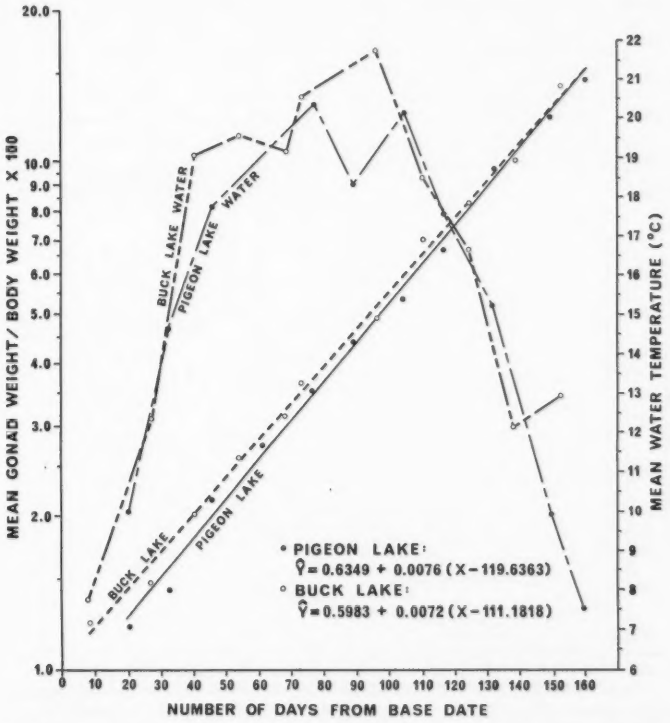
MEAN GONAD WEIGHT/ BODY WEIGHT X 100
MEAN WATER TEMPERATURE (°C)
NUMBER OF DAYS FROM BASE DATE
BUCK LAKE WATER
PIGEON LAKE WATER
BUCK LAKE
PIGEON LAKE
• PIGEON LAKE:
Ŷ = 0.6349 + 0.0076 (X − 119.6363)
◦ BUCK LAKE:
Ŷ = 0.5983 + 0.0072 (X − 111.1818)

FIG. 1. Mean ratio (n = 30) of gonad weight to body weight of mature female lake whitefish (*Coregonus clupeaformis*) and the mean vertical water temperature in Pigeon and Buck lakes at the location of capture. The base date is May 1, 1970. The regression line and equation for each lake is presented.

differences were observed between the size of the eggs produced at three locations within the same gonad.

The present studies support the conclusions of Lawler (1961) on Lake Erie whitefish, that small fish produce fewer eggs than larger fish. Bagenal (1967) concluded from the works of several authors that larger fish produce larger eggs. The results of the present studies revealed that smaller lake whitefish from Pigeon Lake produce larger eggs than the Buck Lake population of larger-sized spawning fish. Christie (1963) reported the fecundity of Lake Ontario whitefish to be 21,794 $\pm$ 3,638 eggs/kilogram. These values are intermediate between the higher value of the faster growing Buck Lake population and the lower value of the slower growing Pigeon Lake population.

Spawning

Both Pigeon and Buck Lake whitefish populations concentrated on a boulder, rubble, and sand substrate to spawn. This substrate occurred on about 16.6% of the bottom of Pigeon Lake and about 15.4% of the bottom of Buck Lake. Concentrated spawning occurred in water of 3.1 m or less in depth in Pigeon Lake and 6.1 m or less in depth in Buck Lake, the depth that the above-mentioned substrate occurred.

An extensive spawning period occurred in both Pigeon and Buck lakes over a wide range of water temperatures (Fig. 3). Ripe female fish were captured on the spawning beds in Buck Lake from October 14 to December 30, 1970, when the bottom water temperature varied from 7.0 to 1.2 C. Active spawning occurred at night but whitefish were observed on the spawning beds during the day in the open water sampling period. Spawning occurred in both open water and under ice cover in both lakes with the highest ratio of ripe females (35%) in Pigeon Lake occurring in the sample at the end of October in open water and in mid December (37% ripe females) under ice cover. The under ice spawners included females that had spawned in previous years (IV-, V-, and VI-yr-old fish). No readsorption of eggs in females was observed in fish from either population sampled from February to April.

Hart (1930) reported that lake whitefish in the Bay of Quinte, Lake Ontario also spawned on a surficial lake sediment of sand, gravel, and boulders. Selection would likely favor whitefish that spawn on this type of substrate since the eggs would be more protected and have a reduced mortality due to wind action in the open water spawning period than eggs deposited on a smoother substrate. Eggs deposited on a rock, gravel, and sand bottom would have more protection from predation by whitefish (Bidgood 1972) or by other species of fish (Hart

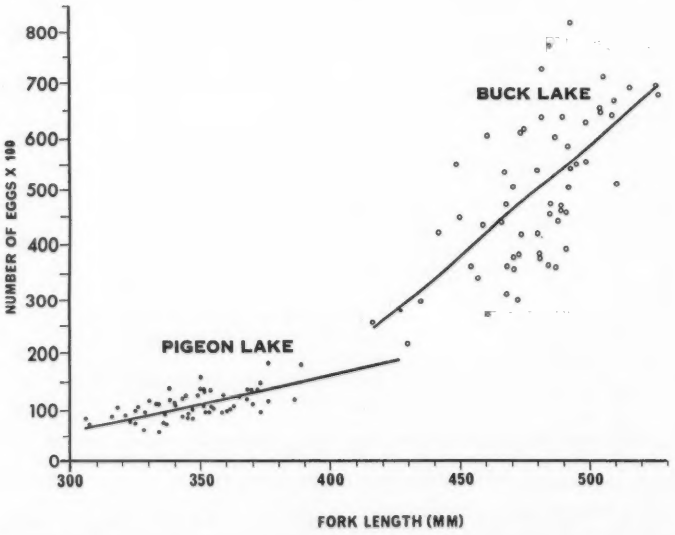

FIG. 2. Fecundity of Pigeon and Buck Lake mature whitefish. Each sample is of 60 fish.

1930) than eggs exposed on a smoother bottom. Lake whitefish were observed spawning on a sand bottom in water 0.7 m in depth in Pigeon Lake. Eggs deposited in this shallow water would be frozen in winter ice that reached a depth of 1 m or more in Pigeon Lake and would not likely contribute to the recruitment of this population of fish. Lake whitefish populations that spawn in both open water and under ice cover in these two study lakes would not likely suffer from reduced recruitment or year-class failures due to loss of eggs exposed to high winds as postulated by Miller (1956). Price (1940) documented the increase in the mortality of lake whitefish eggs incubated under higher temperatures (4 C and higher). Egg mortality in the laboratory experiments in the present studies was noticeably higher under the 4 C incubation water temperature than the 2 C water temperature. Lake whitefish eggs deposited during open water at higher water temperatures in Pigeon and Buck lakes likely have a higher mortality rate than those eggs deposited under ice cover at lower water temperatures.

The Pigeon Lake population appeared to have a longer spawning period than that of the Buck Lake population. Bidgood (1973) estimated Pigeon Lake hed 3 times the number of mature fish per unit area as Buck Lake. The larger numbers of spawning whitefish in Pigeon Lake enabled the capture of spawning fish in January. To document spawning in January in Buck Lake would require increased effort and more sampling than undertaken in the present studies.

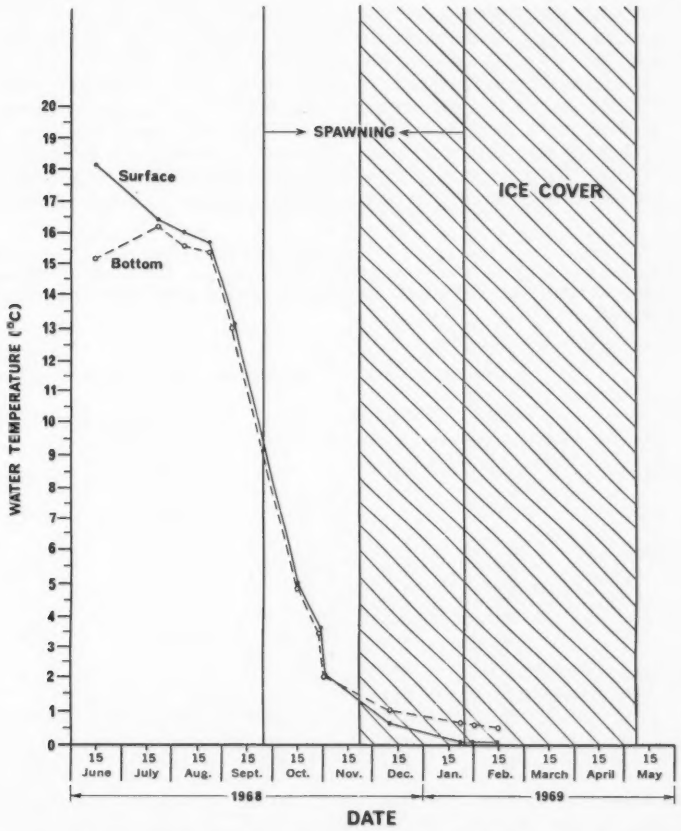

FIG. 3. Spawning period for lake whitefish in Pigeon Lake with reference to the surface and bottom water temperatures on the spawning beds and the formation of ice cover on the lake.

Egg Incubation

The larger Pigeon Lake oviduct eggs remained highly significantly (.01) larger than the smaller Buck Lake oviduct eggs when fertilized, hardened, and incubated to the eyed-egg stage in laboratory experiments. The mean diameter of the Pigeon Lake incubating eggs varied from 2.63 to 2.72 mm, whereas that of the Buck Lake eggs varied from 2.44 to 2.46 mm. The eyed-egg samples did not differ in size from the hardened egg samples of both populations. No differences were observed in the size of the eggs when the Pigeon Lake eggs were spawned, hardened, and incubated in Buck Lake water or the Buck Lake eggs were spawned, hardened, and incubated in Pigeon Lake water.

The trays of eggs, when suspended in enclosed tanks in the incubation trough, were subjected to a minimal water flow to sustain high oxygen tensions. These experiments more closely approximate the incubation of eggs in the two lakes under study. Eggs rolled in jar cultures under the same temperature regime hatched sooner and had a narrower period of hatching than those incubated simultaneously in trays. When the eggs are rolled, adhesive and cohesive friction likely impacts thermal units to the eggs and reduces the incubation time.

The incubation period of the larger Pigeon Lake eggs did not appear to appreciably differ from that of the smaller Buck Lake eggs under the three different egg incubation temperature regimes (Table 1). Eggs continuously incubated at 4 C eyed earlier than those incubated at 2 C for about 19 days, then incubated at 4 C for the duration of the experiment, but the period of incubation to the occurrence of the modal hatch differed by only about 17 incubating days. Eggs incubated continuously at 2 C eyed and hatched later than those incubated at higher temperatures.

The incubation period for whitefish eggs was prolonged by low water temperatures prevalent under ice cover in the shallow water spawning grounds in Pigeon and Buck lakes but was accelerated by the warming of the water in the spring as the ice receded from the shores (Fig. 4). In the 1971–72 experiments, eggs incubated at 2 C for 70–76 days then raised to 4 C for the duration of the experiment all hatched before the ice would have left both lakes. Eggs incubated continuously at 2 C had modal hatching occurring after the ice left both lakes. In Pigeon and Buck lakes, the egg-incubation period would be longer under ice cover since the bottom water temperature on the spawning grounds of both lakes approached 1 C. As the ice

TABLE 1. Incubation period (days) for lake whitefish (*Coregonus clupeaformis*) eggs from Pigeon and Buck lakes to the occurrence of eyed eggs, first hatch of fish, and occurrence of modal hatching (>400 fish) when incubated under three different temperature regimes.

	Incubation regime		Accumulated days from fertilization		
Sample	Days	Temp (*C*)	Eyed	First hatch	Modal hatch
Pigeon Lake	D[a]	4	30	107	156
Buck Lake	D	4	32	83	144
Pigeon Lake	18	2			
	7	2.5			
	7	3.0			
	7	3.5			
	D	4.0	48	107	162
Buck Lake	21	2			
	7	2.5			
	7	3.0			
	7	3.5			
	D	4.0	52	107	161
Pigeon Lake	D	2.0	48	132	191
Buck Lake	D	2.0	51	125	193

[a]Duration of experiment.

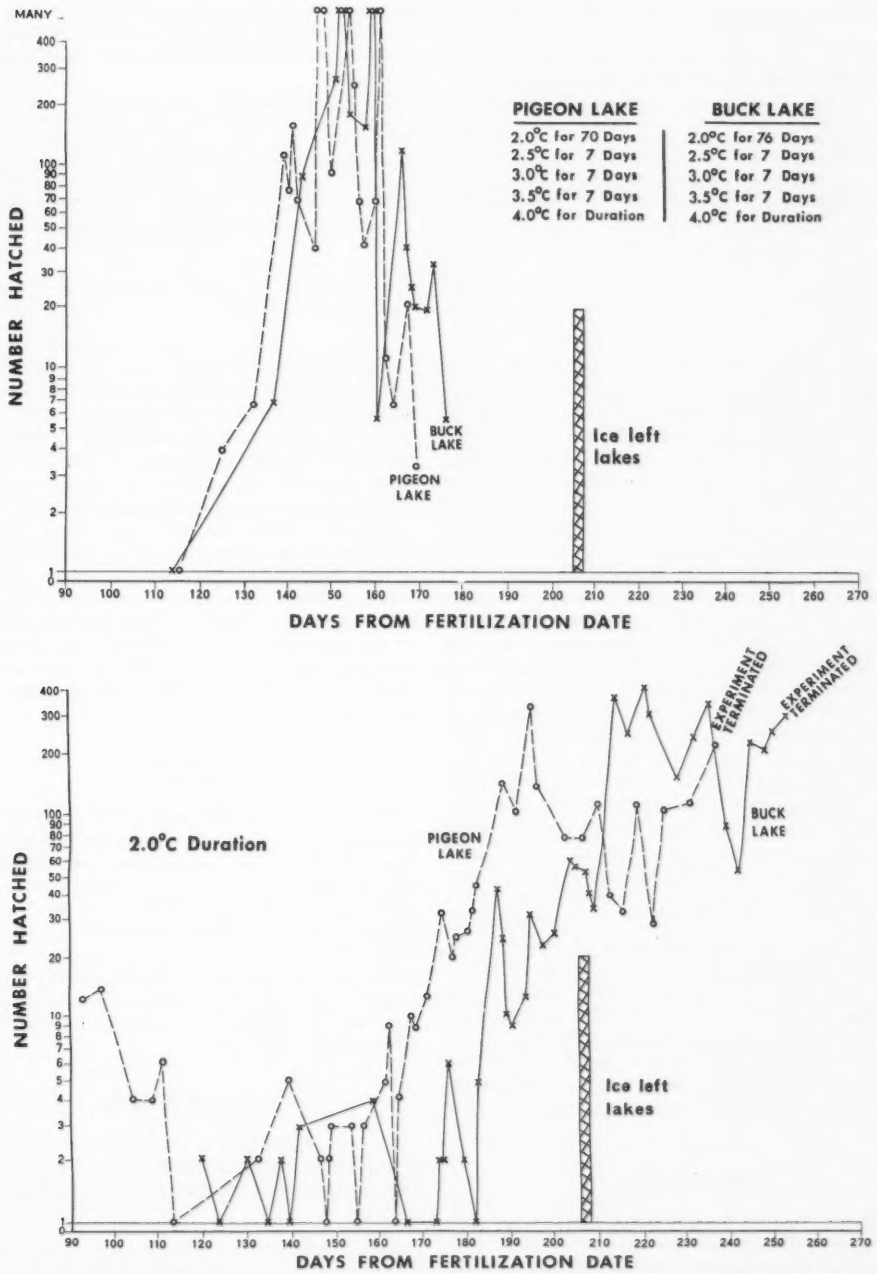

FIG. 4. Number of fish hatching from Pigeon and Buck Lake whitefish eggs incubated under two different temperature regimes. The hatching period in the experiments relative to the date when the ice left both lakes is indicated.

TABLE 2. Mean total length (mm) of Pigeon Lake (PL) and Buck Lake (BL) lake whitefish emerging from eggs incubated at 2 C. The days of incubation to hatching are subscript to the symbols for each lake. Any two means not underlined by the same line are significantly different. Each mean was calculated from the measurements of thirty fish.

Lake — Incubation days									
BL_{231}	PL_{231}	BL_{216}	PL_{216}	PL_{174}	PL_{202}	BL_{202}	BL_{174}	PL_{183}	BL_{183}
11.84	11.74	11.65	11.50	11.48	11.46	11.19	11.12	11.10	11.03

melted from the shore of the lakes and the water temperature increased, the rate of development and hatching of the eggs would be accelerated. Meter trawls along the shore of Buck Lake as the ice receded from the shore yielded newly hatched young-of-the-year (y-o-y) whitefish. The modal hatch of whitefish in these lakes is likely coincident with the ice receding from the shoreline spawning grounds in these two lakes.

The reproductive potential of lake whitefish that spawn in the shallower waters of these two eutrophic lakes would be greater than that of whitefish spawning in deeper waters. Price (1940) found an increase in whitefish egg incubation mortality as incubating water temperatures approached and exceeded 4 C and found maximum egg survival at an incubating water temperature of 0.5 C. The winter bottom water temperatures in the deeper waters of these two eutrophic lakes (Bidgood 1973) would cause high egg incubation mortality. Braum (1967) discussed higher larval mortality when larval fish shift from yolk to an exogenous food source under conditions of a shortage of suitable food and poor visibility. Eggs laid and incubated in deeper, warmer waters would hatch under ice cover when visibility is reduced and low standing crops of zooplankton prevail in these two eutrophic lakes (Bidgood 1973). Eggs deposited in shallow waters would have retarded incubation under lower water temperatures and accelerated development to hatching in the spring as the ice recedes from the shore and the water warms. Hatching would likely coincide with the commencement of zooplankton pulses in the spring.

Hatching Size

Both the smaller Buck Lake whitefish eggs and the larger Pigeon Lake eggs yielded similar sized y-o-y when incubated for the same period of time at 2 C (Table 2). Eggs from both populations of fish that incubated for longer periods of time before hatching produced larger fish ($r=0.81$). Earlier hatching eggs produced y-o-y fish with noticeably larger yolk sacs. These fish remained on the bottom of the rearing containers relatively immobile for 1–2 wk living off the yolk sac. As the yolk sac became depleted, the mobility of the fish increased and they began feeding on the available brine shrimp.

Bagenal (1967) reported that larger fish eggs produced larger emerging y-o-y. The experiments in the present studies on lake whitefish indicated that the size of the egg under incubation had little effect on the size of the hatching fish but the length of the incubation period influenced the size of the emerging fish. Hart (1930) also reported that late hatching whitefish fry were longer than early hatching fry.

Conclusion

The reproductive potential of the faster growing Buck Lake whitefish population was greater than that of the slower growing Pigeon Lake population. Pigeon Lake had a mature whitefish population about three times that of Buck Lake per unit area (Bidgood 1973) but Buck Lake females produced about 4 times the number of eggs per female. Increased numbers and reduced growth rates of Pigeon Lake whitefish appears to have caused a reduction in numbers and increase in size of eggs produced by females.

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Evaluation of the Swimming Performance of Several Fish Species from the Mackenzie River

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Critical velocities of 17 species of fish from the Mackenzie River have been determined from increasing velocity tests in both field and laboratory, and the effects on critical velocity of different acclimation temperatures and of temperature shock were examined. In five species the relation between fatigue time and swimming speed was investigated.

Critical velocity data from 10 species were analyzed by solving the regression equation $V = KL^e$ (where V = critical velocity in cm/s, L = fork length, K = constant, e = exponent). Neither acclimation to different temperatures nor temperature shock over a range of ± 7 C from acclimation temperature had a significant effect on critical velocity. Intraspecific variation was found to be unrelated to maturity, sex, or condition factor.

From a graphical presentation of body length vs. maximum flow rate allowable in a 100-m culvert, it appears that culvert flow rates should be kept below 30–40 cm/s to allow successful passage of the majority of mature individuals of migratory species.

JONES, D. R., J. W. KICENIUK, AND O. S. BAMFORD. 1974. Evaluation of the swimming performance of several fish species from the Mackenzie River. J. Fish. Res. Board Can. 31: 1641–1647.

Les auteurs ont déterminé les vitesses critiques de 17 espèces de poissons du fleuve Mackenzie, au cours d'essais de vitesse croissante, tant sur le terrain qu'au laboratoire, et ont analysé les effets de différentes températures d'acclimatation et d'un choc thermique sur la vitesse critique. Ils ont de plus étudié la relation entre le temps de fatigue et la vitesse de nage.

Les données sur la vitesse critique de 10 espèces ont été analysées par solution de l'équation de régression $V = KL^e$ (dans laquelle V = vitesse critique en cm/sec, L = longueur à la fourche, K = constante, e = exposant). Ni une acclimatation à des températures différentes, ni un choc thermique sur une gamme de ± 7 C à partir de la température d'acclimatation n'ont d'effet significatif sur la vitesse critique. On constate que la variation intraspécifique n'est pas reliée à la maturité, au sexe ou à l'indice d'embonpoint.

Une représentation graphique de la longueur du corps vs le maximum permissible du taux d'écoulement dans un drain de 100 m semble indiquer que les taux d'écoulement dans le drain devraient être maintenus à moins de 30–40 cm/sec pour permettre le passage réussi de la majorité des individus mûrs des expèces migratrices.

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THE construction of a highway along the Mackenzie Valley involves crossing a large number of small rivers, most of which are spawning grounds for fish. Faulty culvert design in these crossings, allowing excessive water flow rates, can create insurmountable barriers to upstream fish migration (Clay 1961; Metsker 1970; Sakowicz and Zarnecki 1954). To assist in the preparation of design guidelines which would minimize environmental damage from this cause, experiments were carried out to determine swimming performance of a total of 17 species of fish found in the Mackenzie River system. The projected route calls for culverts of up to 100 m in length, and of the possible measures of swimming performance, the maximum velocity that can be maintained for 10 min (critical velocity) was chosen as the most appropriate. Clearly the much higher transient burst speed would not carry a fish through culverts of the length proposed, while the indefinitely maintainable cruise speed would probably be too low for any economically feasible culvert design. Accordingly, critical velocities were determined with both laboratory and field equip-

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ment, and the results for each species analyzed with respect to body length.

On migration fish may encounter large environmental temperature changes, so the effects of such changes on swimming performance were also studied. Some determinations were also made of time to fatigue at speeds near the critical velocity, up to a limit of 100 min. However, priority in the available time was given to the critical velocity determinations, and consequently few fatigue or temperature experiments were performed.

Materials and Methods

Experiments were carried out on the following species of fish, all obtained from the Mackenzie or its tributaries: burbot (*Lota lota*), northern pike (*Esox lucius*), yellow walleye (*Stizostedion vitreum vitreum*), Arctic grayling (*Thymallus arcticus*), flathead chub (*Platygobio gracilis*), inconnu (*Stenodus leucichthys nelma*), longnose sucker (*Catostomus catostomus*), white sucker (*Catostomus commersoni*), humpback whitefish (*Coregonus clupeaformis*),[1] broad whitefish (*Coregonus nasus*), Arctic char (*Salvelinus alpinus*), Arctic cisco (*Coregonus autumnalis*), least cisco (*Coregonus sardinella*), emerald shiner (*Notropis atherinoides*), trout-perch (*Percopsis omiscomaycus*), goldeye (*Hiodon alosoides*), and mountain whitefish (*Prosopium williamsoni*). Of these 17 species, burbot, broad whitefish, mountain whitefish, Arctic char, and Arctic cisco were examined only in the laboratory, whereas only field experiments were performed on inconnu, flathead chub, least cisco, goldeye, trout-perch, and emerald shiner. All other species were examined at both sites. In seven species, size range or number of specimens was too small to allow use of regression analysis.

The fish were caught by staff of the Fisheries and Marine Service at Fort Simpson, Norman Wells, Arctic Red River, and Aklavik. Those caught at Fort Simpson were held for 24–48 h without food in pens moored in the Mackenzie before use in the field apparatus. Fish from the other stations were deprived of food for 3 days before being sealed individually in polythene bags containing oxygen and water, packed in styrofoam boxes with ice packs, and air-freighted to Vancouver for laboratory tests. Transit times were normally less than 24 h and mortality was below 10%, though occasional longer transit times resulted in sharply increased mortality. Fish were held in 2000-liter tanks, and treated with nitrofurazone routinely and with salt, when necessary, to reduce fungal infection. They were fed on trout pellets and brine shrimp (*Artemia salina*), and deprived of food for 24 h before use in any experiment.

Preliminary Tests

Settling period — In all experiments an initial settling period at a flow rate of 10 cm/s was allowed for the fish to become accustomed to their surroundings and to minimize the effects of handling. To ascertain how long this period should be, critical velocities were measured after settling periods of 1, 2, 12, and 16 h for Arctic grayling and longnose suckers. No significant differences were found in the critical velocities measured under these conditions, and all fish were therefore allowed 1 h in the tube before any increase in velocity.

Time between velocity increments — Critical velocities of longnose suckers and Arctic grayling were measured using 10-min and 20-min increment periods. The results showed no significant difference between critical velocities measured under these two conditions and all critical velocity determinations were made using 10-min increments, thus allowing more replicates in the time available.

Field Experiments

Only ambient-temperature critical velocities were measured in the field. The apparatus used consisted of a 10.2-cm pump connected via flow control valves and 15.3-cm hose to a 25.4 cm ID plexiglass tube 152 cm in length, with 10° expansion and contraction cones for coupling to the 15.3-cm plumbing. A series of three 0.6-cm mesh grids at the upstream end of the 25.4-cm section introduced microturbulence in the plexiglass tube, resulting in an essentially flat velocity profile as confirmed by dye injection and by measurement of the flow rate at different points on the cross section using an Ottmeter. At the downstream end an electrified grid (5–10 V AC) provided the stimulus to swim, and the upstream part of the tube was covered in black polythene to allow visual orientation by the fish. Water speed in the tunnel was measured by a modified Aqua-Log flowmeter, previously calibrated in a Brett-type respirometer (Brett 1964). Speeds of up to 100 cm/s could be achieved reproducibly in the plexiglass tunnel. The entire apparatus was mounted on a raft moored in the Mackenzie. As the through-flow system pumped water directly from the river, fish in the tunnel were exposed to the same water as in the holding pens and problems of controlling water temperature and pO_2 were avoided.

The same procedure was followed in all experiments. With the water flow adjusted to 10 cm/s and the grid electrified, between one and four fish (depending on size) were introduced to the tube via an access port and left for an hour. At the end of this time, velocity was increased in standard steps of 10 cm/s at 10-min intervals. As fish fatigued they were carried back to the grid, from which they were removed through the access port. Critical velocity was determined as described below. After fatigue the fish were weighed, measured, and sexed, most fish being used only once.

Laboratory Experiments

These were performed using a closed-circuit respirometer with a 8.9-cm ID working section and a maximum water speed of 100 cm/s. Experiments fell under two main headings:

[1]Classification taken from McPhail and Lindsey 1970.

Increasing velocity tests — These were essentially the same as described above for the field equipment, except that due to the much smaller tube, usually only one fish could be run in each determination. This allowed the speed increments to be adjusted so that a critical velocity predicted on the basis of preliminary experiments would be attained in six increments. Water pO_2 was maintained by a slow flow of fresh water into the respirometer circuit and monitored using a Beckman oxygen electrode and analyzer. After fatigue, fish were weighed, measured and tagged, and returned to the holding tanks.

Most of these experiments were performed at the same temperature as that of the holding tanks. To determine any effect of a sudden change in temperature, the water temperature in the respirometer was changed during the initial 1-h settling period by admitting water from a temperature-controlled reservoir. All fish in these experiments had been previously tested at 12–13 C and results were expressed as percent of their performance at that temperature.

Fixed velocity tests — These experiments used 132 fish for which critical velocity had been previously determined. The procedure was a modification of that described by Brett (1967). After a period of 1 h at 10 cm/s, the water speed was increased in five steps, each lasting 3 min, to a test speed of between 60 and 90% of the critical velocity. Time to fatigue at this speed was then recorded, up to a maximum of 100 min. Water temperature was the same as that in the previous critical velocity determination for a given fish, and the pO_2 was maintained at air saturation throughout. After fatigue, the fish was removed, weighed and measured, retagged, and returned to the holding tanks.

Analysis of Data

Critical Velocity

Few fish swam for 10 min at their final increment. In this case the critical velocity was determined by interpolation as described by Brett (1964):

$$C.V. = V_P + \left[(V_F - V_P) \times \frac{t_F}{t_I} \right]$$

where V_P = penultimate water velocity (cm/s)
V_F = final water velocity (cm/s)
t_F = time to fatigue at V_F (s)
t_I = time between velocity increments (s)

For fish with a cross section greater than 10% of the tube area a velocity correction was made for partial blocking of the tube using the formula

$$C.V._2 = C.V. \left[1 + f \frac{A_F}{A_T - A_F} \right]$$

where C.V. = uncorrected critical velocity (cm/s)
$C.V._2$ = corrected critical velocity (cm/s)
A_F = cross section of fish (cm^2)
A_T = cross sectional area of the tube (cm^2)
f is a factor taken to be 0.8 in the present work. For a discussion of this, see Webb (1970).

Previous workers have shown critical velocity to vary as

$$V = KL^e$$

where V = corrected critical velocity (cm/s)
K = constant
L = body length (cm)
e = exponent

(Bainbridge 1960, 1962; Blaxter and Dickson 1959; Brett 1964, 1965; Fry and Cox 1970).

The critical velocity data were therefore analyzed, where possible, to allow determination of K and e for each species. Some species could not be obtained in sufficient numbers for regression analysis and in these cases mean values for size-classes are given.

Where the material allowed, data from a given species were grouped as follows

	Unclassified (with regard to maturity)	Immature	♂	♀
Laboratory 7 C	a_1	a_2	a_3	a_4
Laboratory 12 C	b_1	b_2	b_3	b_4
Field 12 C	c_1	c_2	c_3	c_4
Field 19 C	d_1	d_2	d_3	d_4

and lines and columns tested against one another by analysis of covariances.

Where horizontal or vertical groupings showed significant differences, separate regression lines were drawn for each grouping. Fortunately, this did not often occur, and in most cases all data for a given species could be pooled to yield a final regression equation. Pearson product–moment correlation coefficients were determined for the data in each final regression equation to define the amount of critical velocity variance explained by the regression, thus defining the degree of confidence that could be placed in each equation.

Temperature Shock

Results were calculated as C.V. at experimental temperature/C.V. at acclimation temperature (12–13 C), expressed as a percentage. This value was then plotted against the experimental temperature and a linear regression computed for the data.

TABLE 1. Relationship between fork length, weight, and critical velocity for 10 species of Mackenzie River fish.

Species	*n*	Length range (*cm*)	Weight range (g)	Condition factor[a]	Weight/length correlation coefficient	Length–velocity regression ($V = KL^e$) K	e	Length–velocity correlation coefficient	*p*-value for correlation coefficient	Remarks
Pike	192	12–62	7–1800	0.66±0.01	0.96	4.9	0.55	0.441	0.001	Regression on 12 C lab. data only — insufficient numbers in other groups
Walleye	54	8–38	4–500	0.98±0.02	0.94	13.07	0.51	0.004	0.1	Regression on 18–20 C field data — insufficient numbers in other groups
Grayling	94	7–37	1.5–800	1.03±0.02	0.97	36.23	0.19	0.221	0.02	Includes all groups except 7 C lab. data
	11	21–34	90–500	1.02±0.03	–	91.64	–0.14	–0.104	0.1	
Flathead chub	28	17–30	40–300	0.90±0.02	0.98	6.42	0.67	0.308	0.1	No lab. data — insufficient data for ANCOVA but all data pooled
Inconnu	22	8–41	4–700	0.80±0.04	0.93	30.3	0.75	0.176	0.1	No lab. data field data pooled after ANCOVA showed no significant group differences
Longnose sucker	169	4–53	0.5–2200	1.03±0.01	0.96	11.03	0.53	0.787	0.0001	All groups pooled after ANCOVA showed no significant group differences
White sucker	20	17–37	50–550	1.37±0.21	0.90	10.03	0.55	0.501	0.02	No lab. data — field data pooled after ANCOVA showed no significant group differences
Burbot	56	12–62	7–1100	0.51±0.01	0.96	30.6	0.07	0.045	0.1	No field data — lab. data pooled after ANCOVA showed no significant group differences
Humpback whitefish	159	6–51	2–1500	1.09±0.02	0.94	18.2	0.35	0.36	0.0001	All groups pooled after ANCOVA showed no significant group differences
Board whitefish	33	6–33	1–500	1.09±0.06	0.97	9.7	0.45	0.50	0.003	All groups pooled after ANCOVA showed no significant group differences

[a]Condition factor $= \frac{100W}{L^3}$ where W = weight (g), L = length (cm).

Fatigue Tests

Data were presented graphically as plots of time to fatigue (minutes) against swimming speed. A fixed point regression line was calculated on the 10 min, 100% C.V. point. The maximum time period of these tests was 100 min, and any fish not fatigued in this time was treated as fatiguing at 100 min. Clearly this could lead to spurious results if too low a test velocity was chosen. Accordingly, fish still swimming at 100 min were rejected if their speed was less than 90% of the mean of the two lowest speeds at which individuals of the same species fatigued within the 100-min period. All swimming speeds were expressed as percent of C.V. as determined in increasing-velocity tests.

Results

Critical Velocity Tests

Significant correlations of length and critical velocity were obtained in six species, whereas in five, correlation coefficients were not significant at the 5% level (Table 1). For seven species (Table 2), the number of replicates was too small to allow regression analysis and mean values only are given, ±1 SE of the mean where appropriate.

Temperature Effects

No significant effects of temperature shock were shown in experiments on 15 burbot, 28 northern pike, 23 Arctic grayling, 10 Arctic char, and 22 longnose suckers. In all cases, when the critical velocity attained at the test temperature (expressed as percent of the previously determined C.V.) was plotted against temperature, the slope of the line obtained was not significantly different from zero.

No significant evidence was found for any influence of acclimation temperature between 7 and 20 C on swimming performance in the species tested. Although the 7 C laboratory data for Arctic grayling were significantly different from other groups, the group correlation coefficient was not itself significant. A similar situation occurred with northern pike, where the only significant regression was found in the 12–13 C laboratory data. At present, both findings can be ascribed to insufficient data.

TABLE 2. Mean fork length and critical velocity for seven species of Mackenzie River fish obtained in numbers too small for regression analysis.

Species	Mean fork length (*cm*)	Mean critical velocity (*cm/s*)	*n*
Arctic char	35.5±1.2	100.2±3.0	11
Mountain whitefish	30.4±1.5	42.5±6.5	9
Arctic cisco	42.1	80	4
Emerald shiner[a]	6.5	59	4
Trout-perch[a]	7.2	55	3
Goldeye	22.5	60	2
Least cisco	29.5	60	2

[a]It is possible that these small fish were taking advantage of undetected zones of slow flow in the field tunnel.

Fatigue Tests

Fixed-velocity tests were conducted on 132 fish but data fitting the constraints outlined above were obtained for only 9 northern pike, 19 longnose suckers, 21 burbot, 11 Arctic grayling, and 5 Arctic char. Time to fatigue was plotted against swimming speed, and although none of the regression lines calculated were significant, the data suggest that for longnose sucker, burbot, and pike, the highest speed that can be maintained for 100 min is 60% of the critical velocity, whereas in char and grayling the figure is about 80% of the critical velocity.

In view of the large number of replicates, the wide scatter and low correlation shown in critical velocity vs. length plots was surprising. This variability could not be accounted for in terms of temperature, sex, maturity, or location (laboratory or field). To test whether such extreme variability was due to stresses of handling and transport or was inherent in wild populations, critical velocities of two samples of hatchery-reared and wild-caught rainbow trout (*Salmo gairdneri*) were compared (Table 3). Range and standard error of critical ve-

TABLE 3. Critical velocities for wild-caught and hatchery-reared rainbow trout (*Salmo gairdneri*).

	Wild-caught $n = 6$	Hatchery-reared $n = 6$
Length (mean ± 1 SE)	30.58±1.27 cm	32.75±1.2 cm
(Range)	27.5–36.5 cm	31.0–34.5 cm
Critical velocity (mean ± 1 SE)	66.57±6.29 cm/s	90.97±2.47 cm/s
(Range)	47.10–83.2 cm/s	83.3–97.9 cm/s

locities of the wild-caught fish were over twice those for the hatchery fish. As both groups had been kept in the same conditions for 8–10 wk and fed regularly, it seems that the variability in the wild-caught sample was inherent and not due to trauma, and this probably applies to all the wild-caught stocks used in this work.

Discussion

Although much higher swimming speeds than those found in the present study have been reported in the literature (e.g. Wales 1950; Gray 1953; Sakowicz and Zarnecki 1964), these high speeds were in the short duration "burst" range. As pointed out earlier, such sprint performance cannot be maintained long enough to carry a fish through a long culvert. On the basis of a 10-min transit time, curves were constructed to show the smallest size of each species that could be expected to pass upstream through a 100-m culvert at various water velocities (Fig. 1). The curves were derived as follows: to make 100-m headway in 10 min requires a ground speed (= swimming speed–water speed) of 17 cm/s, i.e. for 10-min transit time,

$$\text{critical velocity–water velocity} = 17 \text{ cm/s}$$

but

$$\text{critical velocity} = K L^e \text{ where } \begin{array}{ll} L & = \text{length (cm)} \\ K & = \text{constant} \\ e & = \text{exponent} \end{array}$$

so

$$K L^e = \text{water velocity} + 17$$

$$L^e = \frac{\text{water velocity} + 17}{K}$$

$$L = e\sqrt{\frac{\text{water velocity} + 17}{K}}$$

This curve was then plotted for each species in which K and e were determined.

Some caution should be used in interpreting these curves, as they are derived from the regression equations given in Table 1, and of these only those

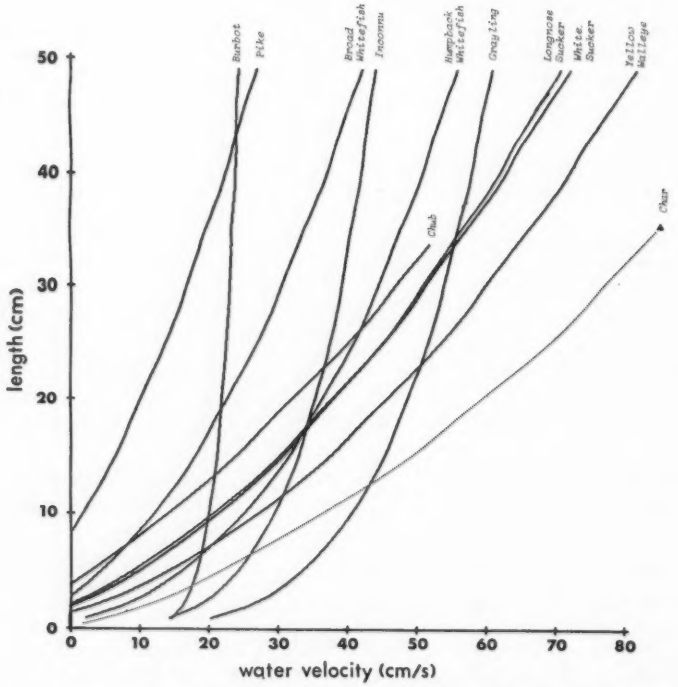

FIG. 1. The relationship between fork length and ability to move 100 m in 10 min against water velocities up to 80 cm/s. The curve for Arctic char (*Salvelinus alpinus*) is derived from the equation $V = 17\ L^{0.5}$ (Jones 1971) and ▲ represents the measured mean values for length and critical velocity.

for northern pike, Arctic grayling, longnose and white suckers, and humpback and broad whitefish are significant at the 5% level. However, the non-significant curves are in the same range, and it seems unlikely that they are seriously inaccurate. The curve for Arctic char was derived using the length–velocity relation obtained for other salmonids by Jones (1971). The point representing mean values of length and critical velocity for Arctic char obtained in the present study is also shown.

For any point on a curve, a fish of the size indicated would be fatigued after 10 min and would thereafter be unable to make any sustained efforts for some time (Paulik et al. 1957). These water velocities therefore represent the maximum permissible for culverts of 100 m in length, in order for fish of the size specified to pass through. For shorter culverts, the curves would be the same shape but moved to the right. For example, for a 50-m culvert, the ground speed need be only about 8 cm/s, and thus the curves would shift to the right by (17–8) cm/s. This relation holds until culvert lengths are such that maximum burst speed becomes significant. For example, the 33-cm *Catostomus occidentalis* described by Wales (1950) would just pass a 9-m culvert with a flow of 150 cm/s, but for it to pass a 15-m culvert the water velocity could be only 30 cm/s.

Although none of the temperature data yielded significant results, a tendency was shown in some species for large fish to swim more slowly at lower temperatures. This was particularly apparent with northern pike, yellow walleye, and Arctic grayling, and a closer study of the change in swimming performance with temperature would probably be rewarding in these species. This effect seems not to apply to young fish, and Brett (1967) found fingerling sockeye to be almost unaffected by temperature between 10 and 20 C.

From Fig. 1 it is possible to predict with reasonable confidence the size-class of fish of a given species that can pass through a given culvert. However, in view of the great variability shown in swimming speed, some selection is certain to occur at culverts. At present it is impossible to predict what effect such selection for swimming speed would have on the gene pool, but there seems no reason to believe that it would be wholly beneficial. To avoid the possibility of deleterious changes in the population, guidelines for culvert water velocity should be set far lower than has been thought necessary in the past.

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Effect of Temperature on Accumulation of Methylmercuric Chloride and *p,p'*DDT by Rainbow Trout (*Salmo gairdneri*)[1]

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REINERT, R. E., L. J. STONE, AND W. A. WILLFORD. 1974. Effect of temperature on accumulation of methylmercuric chloride and *p,p'*DDT by rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 31: 1649–1652.

Amounts of mercury and DDT residues accumulated from water by yearling rainbow trout (*Salmo gairdneri*) in the laboratory increased as water temperature increased. Fish exposed to methylmercuric chloride at concentrations of 234–263 parts per trillion for 12 wk at 5, 10, and 15 C accumulated 1.19, 1.71, and 1.96 ppm; fish exposed to *p,p'*DDT at concentrations of 133–176 parts per trillion accumulated 3.76, 5.93, and 6.82 ppm. Concentrations of mercury accumulated by the fish were significantly different ($P < 0.01$) at each of the three temperatures, and the concentrations of DDT were significantly different at 5 and 10 and 5 and 15 C. Throughout the period of exposure, the concentration factors (concentration of contaminant in the fish/concentration in water) at each of the three temperatures were far higher for *p,p'*DDT than for methylmercuric chloride.

REINERT, R. E., L. J. STONE, AND W. A. WILLFORD. 1974. Effect of temperature on accumulation of methylmercuric chloride and *p,p'*DDT by rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 31: 1649–1652.

Les quantités de mercure et de résidus de DDT accumulées à partir de l'eau par des truites arc-en-ciel (*Salmo gairdneri*) de l'année augmentent en fonction de l'élévation de la température de l'eau. Les poissons exposés au chlorure méthyl-mercurique à des teneurs de 234–263 parties par trillion durant 12 semaines à 5, 10 et 15 C accumulent 1.19, 1.71 et 1.96 ppm; les poissons exposés à *p,p'*DDT à des teneurs de 133–176 parties par trillion accumulent 3.76, 5.93 et 6.82 ppm. Les concentrations de mercure accumulées par les poissons sont significativement différentes ($P < 0.01$) à chacune des trois températures, et les concentrations de DDT le sont également à 5 et 10, et à 5 et 15 C. Durant toute la durée de l'exposition, les facteurs de concentration (concentration de la substance contaminante dans le poisson/concentration dans l'eau) à chacune des trois températures sont beaucoup plus élevées pour *p,p'*DDT que pour le chlorure méthyl-mercurique.

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THE ecological effects of using natural surface waters for the dissipation of waste heat produced during the generation of electric power have been discussed by a number of authors (Coutant 1970; Edsall and Yocom 1972). Although a number of these studies concerned the effects of increased water temperature on fish, apparently none concerned the long-term effects of increased water temperature on the accumulation of contaminants from low concentrations in water. In studies of short-term (36–96 h) effects, Murphy and Murphy (1971) and MacLeod and Pessah(1973) found that the amounts of mercuric chloride and *p,p'*DDT accumulated from water increased with increases in temperature.

This study describes the effect of three temperatures (5, 10, and 15 C) on the amounts of methylmercuric chloride and *p,p'*DDT accumulated from water by yearling rainbow trout (*Salmo gairdneri*). The fish were exposed for 12 wk to concentrations of 234–263 parts per trillion (pptr) of methylmercuric chloride and 133–176 pptr *p,p'*DDT.

Materials and Methods

Fish used in this study were yearling rainbow trout from the Wolf Lake State Fish Hatchery, Mattawan, Michigan. Forty fish were placed in each of 18 fiberglass tanks of 190-liter capacity that had a continuous water flow of 2 liters/min. The water was a blend of three parts well water to one part city water. The city water was passed through a charcoal filter to remove chlorine. Water samples were analyzed at weekly in-

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tervals for dissolved oxygen, total hardness, and pH. Dissolved oxygen at each of the three temperatures remained above 88% saturation throughout the study. Total hardness ranged from 242 to 292 mg/liter and pH from 7.4 to 7.9. Water temperatures in the tanks were increased or decreased at a rate of about 1 C per day until final acclimation temperatures of 5, 10, and 15 C were reached. The fish were then held at these temperatures for 2 wk before exposure to methylmercuric chloride or *p,p'*DDT.

The highest test temperature was set at 15 C because this value is near the final preferendum (the temperature near which all individuals ultimately congregate regardless of their thermal experience before being placed in a gradient — Fry 1947) for rainbow trout (13.8 C — Garside and Tait 1958). Although fish can exist for prolonged periods at temperatures substantially above the preferendum, it seems unlikely that fish in natural aquatic systems would be attracted to temperatures appreciably higher than their preferendum.

All fish were fed Oregon moist pellets ad lib.; the average daily intake for fish held in tanks at 5, 10, and 15 C was about 10, 20, and 30 g, respectively. During the experiment, fish held at 10 and 15 C grew faster than those at 5 C. The average weight for all fish at the beginning of the experiment was 30.9 (±3.7) g. At the conclusion of the experiment the average weights (grams) of the exposed and control fish were as follows (standard error in parentheses, N=5):

C	Methylmercuric chloride	*p,p'*DDT	Controls
5	58.8(±4.2)	61.2(±4.2)	62.1(±4.7)
10	94.5(±5.9)	104.1(±6.1)	99.5(±5.8)
15	89.8(±8.9)	89.6(±8.9)	91.2(±9.0)

At each temperature, weights of control fish did not differ significantly from those of fish exposed to the contaminants ($P < 0.05$; Student's *t*-test).

Identical procedures were used for exposing fish to methylmercuric chloride or *p,p'*DDT in water. Nine groups of 40 fish were used for testing each of the contaminants; at each of the three temperatures two groups were exposed to the contaminant and one served as a control. The addition of methylmercuric chloride and *p,p'*DDT into the tanks holding the groups of fish was controlled by two Harvard Apparatus infusion pumps; each pump operated a 20-ml gas-tight Hamilton syringe. One syringe contained 660 ppm methylmercuric chloride dissolved in water and the other contained 660 ppm of *p,p'*DDT dissolved in acetone. A flow of 0.01 ml/min from each of the syringes was mixed with a flow of water of 2 liters/min in separate 6.6-liter buckets. The diluted concentration of contaminant from each bucket flowed to the respective fish tanks through 1.85-m sections of teflon tubing (0.15 mm inside diameter [ID]) at 200 ml/min.

Water samples were analyzed twice weekly to monitor the concentrations of mercury and *p,p'*DDT. Total mercury was determined from a 100-ml water sample that was acidified (5 ml of concentrated $H_2S_2O_8$, 2 ml of concentrated HNO_3, 1 ml of 6% $KMnO_4$, and 2 ml of 0.5% K_2SO_8), heated to boiling, cooled, decolorized by dropwise addition of a 50% $NH_2OH \cdot HCL$ solution, and transferred to a 250-ml gas wash bottle. Mercury vapors were released by reduction with 2 ml of 20% $SnCl_2 \cdot 2H_2O$, followed by aeration with nitrogen. The resulting mercury vapor was carried by the nitrogen stream through a Mg $(ClO_4)_2$ drying tube and collected in a trap consisting of short pieces of gold wire (Willford et al. 1973). The gold trap was heated in a 450-C tube furnace and the mercury vapors were passed through an absorption cell on a Perkin-Elmer Model 403 atomic absorption spectrophotometer for quantitation. Recoveries of mercury from water fortified with methylmercuric chloride averaged 118% (range 90–140%).

Water samples were analyzed for *p,p'*DDT by extracting 1 liter of water with 200 ml of hexane. The mixture was shaken for 3 min and the hexane layer collected in a 250-ml Erlenmeyer flask. The hexane was dried with anhydrous Na_2SO_4 and concentrated to about 1 ml on a water bath, and 1–5 µl of the concentrate was injected into a gas chromatograph for quantitation of DDT residues. Recoveries of *p,p'*DDT

TABLE 1. Average concentration (ppm; standard error in parentheses) of mercury and DDT (*p,p'*DDT and *p,p'*DDE) in rainbow trout (*Salmo gairdneri*) exposed to these contaminants in water for different periods at 5, 10, or 15 C. Each average is for two groups of five fish each.

Time (*wk*)	Contaminants and water temp (*C*)					
	Mercury			DDT (*p,p'*DDT and *p,p'*DDE)		
	5	10	15	5	10	15
0	0.05(0.00)	0.05(0.01)	0.04(0.00)	0.12(0.00)	0.11(0.01)	0.12(0.00)
2	0.25(0.01)	0.51(0.03)	0.64(0.06)	0.97(0.10)	1.50(0.16)	1.77(0.10)
4	0.40(0.02)	0.58(0.02)	0.81(0.08)	1.63(0.02)	2.26(0.03)	2.32(0.04)
6	0.54(0.01)	0.76(0.06)	1.09(0.20)	2.27(0.10)	3.58(0.26)	3.74(0.84)
8	0.71(0.03)	1.10(0.04)	1.50(0.08)	2.72(0.04)	3.76(0.14)	4.17(0.17)
10	0.94(0.05)	1.34(0.03)	1.86(0.05)	3.68(0.08)	6.04(0.27)	7.10(0.92)
12	1.19(0.01)	1.71(0.23)	1.96(0.10)	3.76(0.47)	5.93(0.08)	6.82(0.34)

from water fortified with *p,p'*DDT averaged 94% (range 79–125%).

Concentrations of methylmercuric chloride, as mercury, and *p,p'*DDT in the tanks were lower than the calculated value of 330 pptr; during the 12 wk of the study the average concentrations (pptr) of methylmercuric chloride were 263 (±15.3) at 5 C, 258 (±16.2) at 10 C, and 234 (±14.6) at 15 C; the respective concentrations of *p,p'*DDT were 176 (±13.0), 137 (±12.9), and 133 (±8.4). The lower concentrations of *p,p'*DDT than of methylmercuric chloride can probably be explained by the tendency for *p,p'*DDT to adsorb to the walls of the containers and to codistill with evaporating water.

Preparation of fish was identical for analyses of mercury and DDT residues. At 2-wk intervals during the experiment, five fish from each tank were collected, weighed, measured, and stored at –30 C. Before analysis, each group of fish was partly thawed and the five whole fish were homogenized together in a blender to form a composite sample. Concentrations of mercury and DDT residues in the samples were expressed as parts per million (micrograms of contaminant per gram wet weight of fish).

Total mercury in each composite sample of fish that had been exposed to mercury was determined by the combustion–amalgamation technique described by Willford et al. (1973). Duplicate analyses were made on each composite sample.

Two methods of analysis were used in measuring concentrations of DDT residues. In one method, 10-g samples of the homogenized fish were saponified in alcoholic KOH and then extracted with hexane (Reinert 1970). In the second method, a 10-g sample of the homogenized fish was dried with 40 g of Na_2SO_4 and the resulting mixture was packed in a glass column (16 mm ID) and eluted with 100 ml of 5% diethyl ether in petroleum ether (Hesselberg and Johnson 1972). The eluant was evaporated to about 1 ml and brought to a volume of 10 ml with cyclohexane; 2 ml were washed through a 1.3- × 25-cm gel permeation column with cyclohexane to remove fats. This cleanup technique is a modification of the method described by Stalling et al. (1972). The second fraction from the gel permeation column (25–85 ml) was evaporated to a volume that brought a 1- or 2-μl injection quantity within the linear range of the gas chromatograph.

We determined the percentage of oil for all fish analyzed for DDT residues by evaporating 1 ml of the 10 ml cyclohexane extract used for DDT residue analyses in a tared aluminum weighing dish, reweighing the sample on a Cahn electric balance, and calculating the amount of oil. The percentages of oil, which ranged from 4.7 to 8.4, did not increase noticeably during the experiment, nor did the amounts differ among fish held at the three temperatures.

Analyses for DDT residues in fish and water were run on a model 2700 Aerograph gas chromatograph equipped with two Ni^{63} detectors and 0.05-ID × 154-mm glass columns packed with 0.3% OV 101 on 80–100 mesh glass beads. The operating characteristics were: oven, 155 C; injection port and detector, 255 C; and nitrogen flow, 30 ml/min.

Effects of Water Temperature on the Accumulation of Methylmercuric Chloride and *p,p'*DDT

Mercury accumulated by fish increased with exposure time throughout this study; DDT residues appeared to approach an equilibrium after 12 wk of exposure (Table 1). At all exposures, mercury and DDT residues increased as water temperature

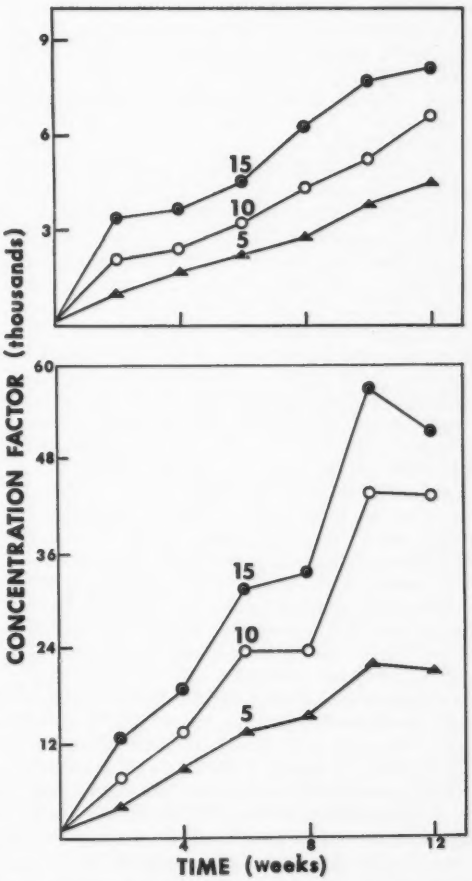

FIG. 1. Concentration factors for rainbow trout (*Salmo gairdneri*) exposed to methylmercuric chloride (*upper panel*) or *p,p'*DDT (*lower panel*) in water at 5, 10, and 15 C. The average concentrations in water (parts per trillion; standard error in parentheses) at 5, 10, and 15 C were 263 (±15.3), 258 (±16.2), and 244 (±14.6), respectively, for methylmercuric chloride and 176 (±13.0), 137 (±12.9), and 133 (±8.4) for *p,p'*DDT.

increased. Analyses of covariance showed significant differences ($P < 0.01$) between the concentrations of mercury accumulated at 5, 10, and 15 C and between the concentrations of DDT accumulated at 5 and 10 C, and 5 and 15 C. After 12 wk, fish exposed to methylmercuric chloride at 5, 10, and 15 C contained an average of 1.19, 1.71, and 1.96 ppm, respectively, and those exposed to *p,p'*DDT contained an average of 3.76, 5.93, and 6.82 ppm. Concentrations of mercury and DDT residues in control fish were closely similar at each of the three temperatures and did not increase during the experiment; mercury ranged from 0.04 to 0.07 ppm and DDT residues from 0.08 to 0.12 ppm. In the food, concentrations of residues (ppm) ranged from 0.08 to 0.10 for mercury and from 0.03 to 0.08 for DDT.

Two forms of DDT residues, *p,p'*DDT and *p,p'* DDE, were identified in all fish exposed to *p,p'*DDT in water. The percentages of these residues remained about the same regardless of the water temperature or the duration of exposure; throughout the study, *p,p'*DDT contributed 87.6–93.1% of the total DDT residue.

Concentration factors (concentration of contaminant in the fish/concentration in the water) for mercury were much lower than those for DDT residues (Fig. 1). At the end of the experiment, concentration factors for fish exposed to water temperatures of 5, 10, and 15 C were 4532, 6622, and 8049 for mercury residues and 21,363, 43,158, and 51,355 for DDT. The extremely high lipid/water partition coefficient of *p,p'*DDT is probably the single most important factor in explaining the high concentration factor for this compound.

Increases in the amounts of mercury and DDT residues accumulated by the fish as water temperatures increased were probably related to increases in metabolic rate. Although metabolic rates were not measured in the present study, two other studies have suggested a direct relation between accumulation of contaminants from water and metabolic rate. MacLeod and Pessah (1973) reported that during 96 h of exposure the rate of accumulation of mercuric chloride from water increased as water temperature increased. They attributed this increase in concentration to an increase in metabolic rate. Murphy and Murphy (1971) reported that when mosquitofish (*Gambusia affinis*) were exposed to *p,p'*DDT in water at temperatures of 5 and 20 C for 36 h, fish held at 20 C accumulated the most DDT. They found a nearly linear relation between the amounts of DDT residues accumulated by the fish and the amounts of oxygen consumed.

The present study shows that an increase in temperature can increase the rate of accumulation of mercury and DDT from water. The extent of the increase, however, would logically depend on such factors as the amount of increase in water temperature, the amount of time fish are in the warmer water, the initial concentration of contaminants in the fish, and the effects of water temperature on the rate of feeding of fish (and, hence, on the amount of contaminants accumulated from food) and on the rate of excretion. Because all of these factors interact, it is extremely difficult to predict the total effect of water temperature on the amounts and the ultimate concentrations of mercury and DDT accumulated in fish in natural aquatic systems

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Acute Toxicity of Nitrite to Rainbow Trout (*Salmo gairdneri*)

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Flow-through bioassays on the acute toxicity of nitrite to rainbow trout (*Salmo gairdneri*) of four different sizes (2–235 g) showed median lethal concentration (LC50) values for 4 days ranging from 0.19 to 0.39 mg/liter NO_2–N. For 12-g rainbow trout the asymptotic LC50 was 0.14–0.15 mg/liter NO_2–N after 8 days.

RUSSO, R. C., C. E. SMITH, AND R. V. THURSTON. 1974. Acute toxicity of nitrite to rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 31: 1653–1655.

Des essais biologiques à flot continu sur la toxicité aiguë du nitrite à l'endroit de truites arc-en-ciel (*Salmo gairdneri*) de quatre tailles différentes (2–235 g) indiquent des concentrations létales médianes (CL50), après 4 jours, variant entre 0.19 et 0.39 mg/litre de NO_2–N. Chez des truites de 12 g, la CL50 est de 0.14–0.15 mg/litre de NO_2–N après 8 jours.

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THE amount of nitrite being discharged by sewage treatment plants utilizing a nitrification process may raise the concentration of nitrite in a receiving water so that it may be significant to the stream biota. Water reuse systems in some fish hatcheries also employ a nitrification process to reduce ammonia concentrations; where these systems are used, hatchery fish may also be subjected to increased nitrite levels.

There are few published data on nitrite toxicity to fishes. Gillette et al. (1952) observed that the critical range for creek chub (*Semotilus a. atromaculatus*) was 400–2000 mg/liter $NaNO_2$ (80–400 mg/liter NO_2–N). Klingler (1957) reported that 50 mg/liter $NaNO_2$ (10 mg/liter NO_2–N) was fatal to minnows (*Phoxinus laevis*) in 14 days and that 10,000 mg/liter (2030 mg/liter NO_2–N) caused 50% mortality in 1.5 h. Wallen et al. (1957) reported a 24-h LC50 of 8.1 mg/liter $NaNO_2$ (1.6 mg/liter NO_2–N) and 48- and 96-h LC50 values of 7.5 mg/liter $NaNO_2$ (1.5 mg/liter NO_2–N) for mosquitofish (*Gambusia affinis*). More recently, Smith and Williams (1974) observed 55% mortality in 24 h at 0.55 mg/liter NO_2–N for yearling rainbow trout (*Salmo gairdneri*) and 50% mortality in 24 h at 1.60 mg/liter NO_2–N for rainbow fingerlings. They also reported 40% mortality in 24 h for chinook salmon (*Oncorhynchus tshawytscha*) exposed to 0.50 mg/liter NO_2–N.

In this paper we report results of laboratory bioassays carried out to investigate the acute toxicity of nitrite to rainbow trout (*Salmo gairdneri*).

Materials and Methods

Five laboratory flow-through bioassays were conducted to investigate the acute toxicity of nitrite to rainbow trout. Four different sizes of hatchery-reared fish, ranging from 2 to 235 g, were tested at NO_2–N concentrations of approximately 1 mg/liter and less (Table 1). Sodium nitrite (reagent grade) was used as the toxicant; five test tanks at different concentrations and one control tank were used for each bioassay. Acclimation time for the fish to their surroundings

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TABLE 1. Acute toxicity of nitrite to rainbow trout (*Salmo gairdneri*).

Avg wt of fish (*g*)	Concn range tested (*mg/l NO_2–N*)	LC50 (*mg/l NO_2–N*)			Minimum tested level with no mortalities (*mg/l NO_2–N*)		Avg water temp (*C*)	Dissolved oxygen (*mg/l*) Avg (*Range*)
		24 h	48 h	96 h	96 h	240 h		
2.3	0.07–1.09	0.96	0.66	0.39	0.14	0.14	10.8(±0.4)	8.6(7.9–9.1)
11.9	0.10–0.34	–	0.30	0.19	0.10	–	12.6(±0.8)	7.7(5.9–9.3)
12.1	0.11–0.37	–	0.30	0.22	–	–	12.3(±0.9)	7.7(6.0–8.8)
14	0.06–0.90	0.49	0.36	0.27	0.12	–	11.6(±0.8)	5.9(4.8–7.0)
235	0.06–0.32	–	0.30	0.20	0.06	0.06	9.5(±0.3)	8.6(8.1–9.2)

differed among the tests, but in all cases test fish were acclimated to the test dilution water for at least a week, and to the test tanks for at least 2 days prior to the introduction of toxicant. The 14- and 235-g trout were not fed during testing; all other fish were fed a commercial trout feed 4 times daily.

Four of the bioassays were carried out in 64-liter plastic tanks, using serial diluters of the basic design of Mount and Brungs (1967) for toxicant delivery; turnover time of test water was approximately 5 h. One test lasting 10 days was on 2-g trout, using 20 fish in each tank; a second test on 14-g trout used 10 fish in each tank and lasted 4 days; the third and fourth tests were duplicate bioassays on 12-g trout, 20 fish in each tank, and lasted 23 and 24 days.

The fifth bioassay, on 235-g fish, was conducted in 660-liter circular fiberglass tanks; Mariotte bottles were used for toxicant delivery, and test water turnover time was approximately 2 h. The test began with 20 fish in each tank; however, a total of 12 fish escaped from the six tanks during the test (no more than three fish from any one tank), and these were not included in the data.

Ground-spring water from a common source was used for all tests, and was routinely monitored for chemical characteristics. Nitrite concentrations in all test tanks were determined 5 times a week by the method described in Strickland and Parsons (1972). Alkalinity, pH, hardness, ammonia, dissolved oxygen, temperature, and nitrate were determined from 1 to 6 times during each bioassay, according to procedures described in APHA (1971); dissolved oxygen was determined either by the azide modification of the iodometric method or by a Yellow Springs Instrument Co. Model 54-RC D.O. meter.

The average and range of the measured chemical parameters (other than nitrite) in the bioassay test tanks were: pH 7.9 (7.8–8.1), alkalinity 176 (169–195) mg/liter $CaCO_3$, hardness 199 (197–200) mg/liter $CaCO_3$, ammonia nitrogen (NH_3–N) 0.25 (0.00–0.86) mg/liter, and nitrate nitrogen (NO_3–N) 0.24 (0.00–0.89) mg/liter. Dissolved oxygen and temperature conditions are listed in Table 1.

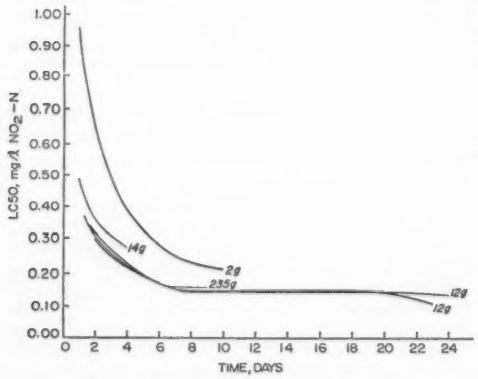

FIG. 1. Toxicity curves from nitrite bioassays on rainbow trout (*Salmo gairdneri*).

Results

Median lethal concentrations (LC50) and the tested nitrite concentrations at or below which no mortalities occurred are presented in Table 1. The 96-h LC50 values for the five bioassays ranged from 0.19 to 0.39 mg/liter NO_2–N. The duplicate bioassays on 12-g trout had similar 96-h LC50 values of 0.19 and 0.22 mg/liter NO_2–N. Both bioassays were continued long enough so that the toxicity curves levelled off, and at 8 days reached asymptotic LC50 of 0.14 and 0.15 mg/liter NO_2–N (Fig. 1). Additional mortalities began to occur on day 19. A preliminary study, not included in Table 1, was conducted using rainbow trout sac fry. One hundred fry exposed to 1.05 mg/liter NO_2–N for 51 h exhibited 50% mortality; there were no mortalities among the 100 control fry.

Discussion

Nitrite oxidizes hemoglobin directly to methemoglobin (Bodansky 1951). Exposure of trout and salmon to nitrite results in methemoglobinemia

(Smith and Williams 1974). Because methemoglobin cannot transport oxygen, fish may die from anoxia. Methemoglobin levels were not determined in the present study, but some fish dying from nitrite poisoning were examined and showed clinical signs typical of those reported previously by Smith and Williams; that is, thymus lesions and chocolate brown-colored blood.

The 2-g trout and sac fry exhibited greater tolerance to nitrite than the larger fish for the time periods reported. Smith and Williams (1974) reported a higher tolerance to nitrite for rainbow trout fingerlings (4.5 g) when compared with yearlings (100 g). Assuming that trout are dying from methemoglobinemia, the higher tolerance to nitrite by young trout may be attributable to the higher oxygen affinity of the hemoglobin in larval and possibly juvenile stages of rainbow trout when compared with adults (Iuchi 1973).

Gillette et al. (1952), Klingler (1957), and Wallen et al. (1957) have reported static bioassay data on nitrite toxicity to mosquitofish (*Gambusia affinis*) and minnows (*Phoxinus laevis* and *Semotilus a. atromaculatus*). Their reported toxicity data for these warmwater fishes are higher than those observed by us or reported by Smith and Williams (1974) for salmonids. A comparison of available data suggests that there may be differences in tolerance to nitrite between salmonids and the more rapidly metabolizing warmwater fishes. In making this comparison, however, it should be noted that there were differences in bioassay conditions, including water chemistry.

The concentrations of nitrite nitrogen that we found to be toxic to rainbow trout in the laboratory are comparable to concentrations observed in fish hatchery water reuse systems (Corps of Engineers 1972) and also to concentrations we have observed in a freshwater trout stream in the area immediately below a sewage discharge point (MSU Fisheries Bioassay Laboratory unpublished data). Although nitrite in a natural stream system is short-lived because of its rapid oxidation to nitrate, nonetheless, for some distance downstream from the discharge point, depending upon the amount discharged and the resident bacteria, it represents a potential toxicant to fishes.

Acknowledgments

This work was supported in part by the U.S. Environmental Protection Agency under grant number R800861. Dr R. Craig performed many of the chemical analyses and assisted with laboratory procedures. We thank Drs K. E. F. Hokanson and W. A. Spoor for helpful comments on the manuscript.

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OBITUARY

John Lawson Hart

1904-1973

Dr John Lawson Hart died on December 6, 1973 at his home in St. Andrews, New Brunswick at the age of 69. With his passing, Canada lost a dedicated aquatic scientist and an able research administrator whose career spanned over half a century.

John Hart was born and educated in Toronto. In his undergraduate years at the University of Toronto he was influenced first by Dr W. A. Clemens, and later by Dr J. R. Dymond, to pursue a career in fisheries biology, and from 1922 to 1925 he studied the life history of the whitefish, mainly in Lake Nipigon. During this early period, according to Dr F. E. J. Fry, John Hart did "a fundamental and pioneering piece of work" in Shakespeare Island Lake in Lake Nipigon by producing "one of the early population estimates that was made of a population of fish" — work that was continued by Dr W. E. Ricker. In recollection, John recently referred to this period, which involved all the vicissitudes of primitive outdoor living and crude scientific equipment, as "one of the very happy times of my life."

In the late 1920s, he continued his studies on whitefish in the Bay of Quinte in Lake Ontario and these formed the basis for his Ph.D. degree, which he received in 1930 from the University of Toronto.

After a brief period as lecturer in zoology at the University of Alberta in Edmonton, he joined the Biological Board of Canada (later the Fisheries Research Board) in 1929 on the invitation of Dr Clemens, who was then director of the Board's research station at Nanaimo. He remained with the Board for 38 years until his retirement in 1967.

His first assignment at Nanaimo was to investigate the Pacific pilchard (California sardine) stocks off British Columbia which were the basis for an important reduction (oil and meal) fishery. From age and growth studies he noted that only the larger and older fish were found off B.C. Through contacts with California scientists, including Dr W. F. Thompson, he became convinced that pilchards spawned only in waters to the south of B.C. He postulated that only the large year-classes, spawned off California and Mexico, reached the B.C. coast in abundance. This classic study enabled him to forecast accurately the decline and collapse of the B.C. pilchard fishery, as the new year-classes became progressively less abundant through either natural causes or overfishing off California.

In the early 1930s Dr Hart also initiated studies on the Pacific herring, another pelagic species about which little was known. He recognized in those early years the urgent necessity of determining the size of fish stocks in order to advise on the permissible catch. He soon concluded that morphometric studies would not be adequate to delineate the intermingling races of Pacific herring, and with the assistance of Dr A. L. Tester he launched an extensive tagging and recovery program which formed the basis for definitive studies by Tester in later years.

In the early 1940s John Hart's interests in marine fisheries changed in response to urgent need for information on dogfish, lingcod, and other groundfish fisheries, which were expanding rapidly to offset wartime shortages of vitamin A and meat products. Sparse scientific data were available on the complex of fishes being caught by the fast-developing otter-trawl fishery, and little was known of the impact of this fishery on long-established hook and line fisheries for lingcod, sablefish, and halibut. To provide answers to these difficult questions John set up a groundfish investigation in 1943 which, through his wise leadership, made significant scientific advances in the years which followed.

His interest in the marine fauna was broad. During his years at Nanaimo he studied, in addition to species previously mentioned, fur seals, capelin, dogfish, butter sole, albacore, amphipods, smelts, and Pacific pompano. He strongly believed that research was not completed until the results were published, and findings from all of his own research are in print. This conviction was impressed upon his staff when he became a research administrator, along with his belief in the importance of making research results available to potential users. As late as 1963 he produced a publication entitled "Useful publications for oyster farmers of the Maritimes." In all he published almost 100 papers, including one in Norwegian.

When John Hart was appointed Director of the Nanaimo Station of the Board in 1950, he initiated new or enlarged research programs in fish physiology, behavior, and parasites. In the early 1950s he participated in the beginnings of the International North Pacific Fisheries Commission, and a few years after moving to the directorship of the St. Andrews Station in 1954 he became closely connected with developments in the International Commission for the Northwest Atlantic Fisheries. He felt strongly that ICNAF's survival depended on instituting effective international controls on fishing. At St. Andrews he was involved in the extensive Canada–U.S. Passamaquoddy Fisheries Investigations from 1956 to 1959. As director, he played an important role in opening up the vast Canadian Atlantic herring fishery, in promoting the exploitation of underutilized Atlantic species, and in initiating studies on the ecology of the coastal ocean bottom — an area which has considerable current importance.

John Hart was a clear thinker and a master of the English language. He always weighed his words before be spoke or wrote. One day in the early 1940's he went into the office of a young scientist who was struggling to compose a difficult paragraph in his first paper. He suggested, "You haven't thought out what you want to say.

Think before you write, and after you've written think and write again." The fledgling scientist, who later became a journal editor, has often recalled this sound advice.

He was above all a man of principle and a gentleman. He was completely honest with his associates and with himself. He was decisive and never went back on his word. At the same time he was open-minded and was influenced by people whose opinion he trusted. He made friends cautiously, and sometimes seemed aloof and reserved on first meeting. He had a broad sense of humor, which often was delightfully puckish in the company of friends.

In 1967, John retired as director of the St. Andrews Station. Soon he became restless and found a new career as a systematist of Pacific fishes, attacking the writing of a new book on the subject with great vigor. His broad interest in and research on the fish fauna of the B.C. coast from the early 1930s gave him a sound basis for writing this book. Never complacent, John worried that in this endeavor he might be "an amateur playing in a professional league." This concern proved unfounded, and in the last months of his life numerous favorable reviews of his book reached him from all over the world. It was the crowning of a highly productive life.

John was active in many international scientific societies throughout his life and was elected a Fellow of the Royal Society of Canada at an early age. But being a humanist as well as a scientist, he found time to participate fully in the Rotary Club in Nanaimo and in the Kiwanis Club in St. Andrews. One of his keenest interests in later years was the establishment of the Passamaquoddy Lodge, a home for senior citizens in St. Andrews.

This year a new government research vessel, the *J. L. Hart*, will be launched on the Atlantic coast, working out of St. Andrews. Nothing could be more fitting in memory of a man who devoted himself to studies of life in Canada's lakes and oceans.

John Hart leaves his wife Olive, his daughter Kathryn Manzer, and two granddaughters, Patricia and Jennifer. They, along with scientists and friends everywhere, mourn his passing.

J. C. STEVENSON

NOTES

Seasonal Succession of Free-Swimming Perciform Larvae in Lake Opinicon, Ontario

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AMUNDRUD, J. R., D. J. FABER, AND A. KEAST. 1974. Seasonal succession of free-swimming perciform larvae in Lake Opinicon, Ontario. J. Fish. Res. Board Can. 31: 1661–1665.

Free-swimming larvae of five perciform species were collected with tow nets in large numbers in Lake Opinicon from May to August of 1969 and 1970. The species appeared in the same seasonal sequence during the 2 yr: first yellow perch (*Perca flavescens*) followed by logperch (*Percina caprodes*), black crappies (*Pomoxis nigromaculatus*), and pumpkinseeds and bluegills (*Lepomis gibbosus* and *L. macrochirus*). Peaks of larval abundance, and also hatching, occurred earlier in 1970, when nest-site temperatures from early May to mid-June showed faster lake warm-up than in 1969.

AMUNDRUD, J. R., D. J. FABER, AND A. KEAST. 1974. Seasonal succession of free-swimming perciform larvae in Lake Opinicon, Ontario. J. Fish. Res. Board Can. 31: 1661–1665.

Nous avons récolté un grand nombre de larves nageuses de cinq espèces de perciformes dans des filets en touée dans le lac Opinicon, entre mai et août 1969 et 1970. Les espèces sont apparues dans la même succession saisonnière les 2 années: d'abord la perchaude (*Perca flavescens*), suivie du dard-perche (*Percina caprodes*), de la marigane noire (*Pomoxis nigromaculatus*), et du crapet-soleil et du crapet arlequin (*Lepomis gibbosus* et *L. macrochirus*). Les sommets d'abondance des larves, de même que ceux de l'éclosion, se sont produits plus tard en 1970, alors que les températures sur le site des nids, du début de mai à la mi-juin, ont indiqué un réchauffement plus rapide du lac qu'en 1969.

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KNOWLEDGE about certain reproductive events in the lives of fish is necessary to interpret the ecology of newly hatched, free-swimming fish larvae. We studied one aspect of their ecology, the seasonal succession of species in Lake Opinicon in 1969 and 1970, including two percids (yellow perch, *Perca flavescens*; logperch, *Percina caprodes*) and three centrarchids (black crappie, *Pomoxis nigromaculatus*; pumpkinseed, *Lepomis gibbosus*; bluegill, *L. macrochirus*). In addition, for pumpkinseeds and bluegills, the two species for which observations were possible, we recorded the following reproductive events at weekly intervals to determine the differences between the 2 yr in times of hatching and becoming free-swimming: dates of first attendance, first eggs and first larvae on nests, and numbers of nests with larvae. These data show the temporal relationship between spawning, hatching, and the subsequent appearance of larvae in open water.

Previous records of occurrence of free-swimming perciform larvae in lakes are limited mainly to

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those of Nordquist (1915), Fish (1932), Faber (1967), Houde (1967, 1969), Werner (1969) and Taber (1969). Nordquist, Fish, and Taber were concerned with their identification while Faber, Houde, and Werner studied their distributional ecology.

Lake Opinicon is a small eutrophic lake in the Rideau Canal system, southern Ontario, and is about 3.7 km (6 miles) long and 0.6 km (1 mile) wide. It attains surface temperatures over 28 C (80 F) in summer, total dissolved solids over 120 ppm, and a maximum depth slightly over 9 m and has a fish fauna of 16 known species.

Materials and methods — For collecting free-swimming larvae, twin conical nets were mounted at the ends of a 3.05-m (10-ft) long wooden frame that was placed across the bow of a boat. The mouth of each net had a diameter of 61 cm and the net tapered over a length of 2.5 m to a diameter of 10 cm and terminated in a 2-liter plankton bucket. Tows were taken with the boat moving at an average speed of 38.5 m/min. Most tows were taken in shallow water parallel to shore but at two stations in the central part of the lake tows were taken both at the surface and at a depth of 3 m. A pair of samples was taken in a 2-min period. Netting was carried out at intervals of about a week at 11 stations in 1969 and at five stations in 1970, when effort was concentrated on the more productive sites. The netting stations were chosen in order to cover a variety of ecological habitats (Amundrud 1970). Netting was carried out at night (2200–0130) since previous workers (e.g. Faber 1963; Noble 1970) found that the larvae aggregate less during darkness. At the end of each tow the young fish were preserved in 5% formalin.

Larvae of yellow perch were identified on the basis of descriptions by Fish (1932) and Mansueti (1964); those of logperch, on the basis of Fish (1932) and Taber (1969). Black crappies were identified on the basis of descriptions of white crappies by Morgan (1954) and Taber (1969). Sunfish were identified on the basis of descriptions by Morgan (1951) and Balon (1959) but it was not possible to separate bluegills from pumpkinseeds, as morphological measurements, including those used by Werner (1966), overlapped. Even larvae taken from known bluegill and pumpkinseed nests had overlapping meristic and morphological features.

For observations of nests a wet-suit, snorkel, and face mask were used at irregular intervals.

Water temperatures were taken with a Wilh. Lambrecht KG Gottingen continuous recorder near the shoreline adjacent to Queen's University Field Station boathouse.

Succession of species — Tow net collections from May to August produced a succession of free-swimming larvae of the five species in large numbers. Yellow perch larvae were collected first each year followed by logperch, black crappies, and finally sunfish (including both pumpkinseeds and bluegills) (Fig. 1). There was no overlapping of yellow perch and sunfish periods of occurrence, but those of logperch and black crappies each overlapped somewhat with those of yellow perch and sunfish and in 1970 occurred almost simultaneously. Each year yellow perch were taken in large numbers for 2–3 wk, both logperch and black crappies in smaller numbers for 2–3 wk, and sunfish in large numbers for about 6 wk. Although we could not distinguish them, our observations of the nests of pumpkinseeds and bluegills indicated that larval pumpkinseeds appeared prior to larval bluegills (see data below). Yellow perch and logperch were present each year in the water when sampling was started, and sunfish when sampling was terminated.

The peaks of larval abundance for the various species occurred earlier in 1970 than in 1969 and appeared to be related to the rate of lake warm-up, for the nest-site area temperatures (Fig. 2) were generally higher from early May through mid-June in 1970 than in 1969. Also, adult pumpkinseeds and bluegills began attending nests and laying eggs earlier, and their larvae appeared earlier in 1970 than in 1969. The dates for the 2 yr were:

	Species			
	Pumpkinseeds		Bluegills	
First attendance	1969	June 5	1969	–
	1970	May 28	1970	June 7
First eggs	1969	June 9	1969	June 24
	1970	June 4	1970	June 15
First larvae	1969	June 15	1969	July 2
	1970	June 11	1970	June 22

The peak numbers of pumpkinseed and bluegill nests with larvae (Fig. 3) also occurred earlier in 1970 than in 1969. However, the peaks of abundance of yellow perch and logperch and those of logperch and black crappies occurred closer together during the faster warm-up year. The data suggest that the faster warm-up of the lake during 1970 induced earlier spawning, which in turn caused the peaks of abundance to occur earlier.

Differences in hatching periods for the 2 yr were indicated by the sizes (Fig. 4) of larvae of the various species at their first appearances and peak abundances. These sizes (4.5–13 mm) represent the late portions of the embryonic periods (eleuterembryonic phase) and most of the larval periods (protopterygiolarval and pterygiolarval phases) of fishes as described by Balon (1971). The early samples of each species indicate that the larvae began hatching a few days earlier and the later samples indicate, for all except yellow perch in both years and logperch in 1970, that they hatched during two or three

periods. The data indicate that hatching in all species began a week or two earlier in 1970 than in 1969. In addition, the periods of occurrence of eleuterembryonic-phase larvae imply that yellow perch, and logperch in 1970, hatched during a short period of a week or two and that the centrarchids (black crappies, pumpkinseeds, and bluegills) hatched during a longer period of 3–4 wk. Hence, in Lake Opinicon, yellow perch appear to spawn the earliest, followed by logperch, black crappies, pumpkinseeds, and finally bluegills.

Discussion — The seasonal succession and patterns of abundance of free-swimming larvae were similar during the 2 yr of study and were similar to those found by Faber (1967) in the limnetic region of two northern Wisconsin lakes. These results suggest that the seasonal periodicity of free-swimming perciform larvae in most small temperate lakes is closely related to the periodicity of several reproductive events preceeding hatching and that the timing for these reproductive events can be locally influenced by annual changes in the rate of lake warm-up.

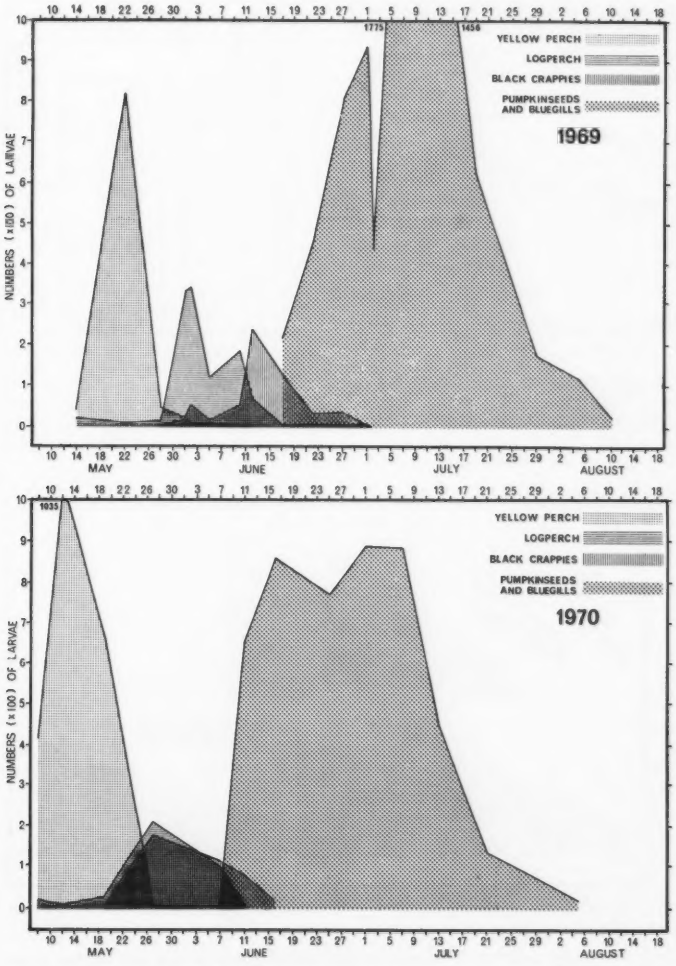

FIG. 1. Numbers of free-swimming perciform larvae collected in Lake Opinicon on various dates during 1969 and 1970.

Of the 11 other species of fish recorded from the lake, larvae and/or juveniles of the following were collected in the tow nets irregularly in small numbers: largemouth bass, *Micropterus salmoides* (mid-June to early August); rock bass, *Ambloplites rupestris* (late June); brook silverside, *Labidesthes sicculus* (mid-July to mid-August); and alewife, *Alosa pseudoharengus* (mid-June to mid-August). A number of cyprinid larvae were collected (early June to late July) but it is not known which species were represented: golden shiner, *Notemigonus crysoleucas*; bluntnose minnow, *Pimephales notatus*; or blackchin shiner, *Notropis heterodon*. Larvae or juveniles of the following were not taken: central mudminnow, *Umbra limi*; northern pike, *Esox lucius*; banded killifish, *Fundulus diaphanus*; and Johnny darter, *Etheostoma nigrum*.

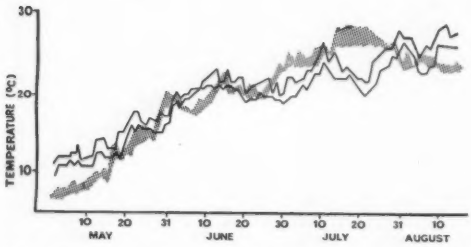

FIG. 2. Maximum and minimum daily temperatures near the shoreline of Lake Opinicon, within the nest-site area, May 1–August 15, 1969 (shaded) and 1970 (solid lines).

This study demonstrated the usefulness of tow net collections of larvae to estimate hatching and spawning periods for several species of fish. It is noteworthy that tow nets can collect perciform larvae with very different modes of reproduction. Yellow perch lay their eggs in long "accordion-folded" strands among debris, etc., logperch lay them broadcast-style and black crappies, pumpkinseeds, and bluegills carefully tend them in nests. Our observations of the depth-distribution of centrarchid nests did not differ significantly from

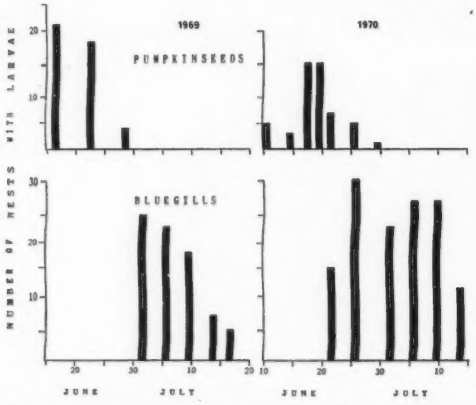

FIG. 3. Observed numbers of nests of pumpkinseeds and bluegills with larvae in Lake Opinicon on various dates during June and July, 1969 and 1970.

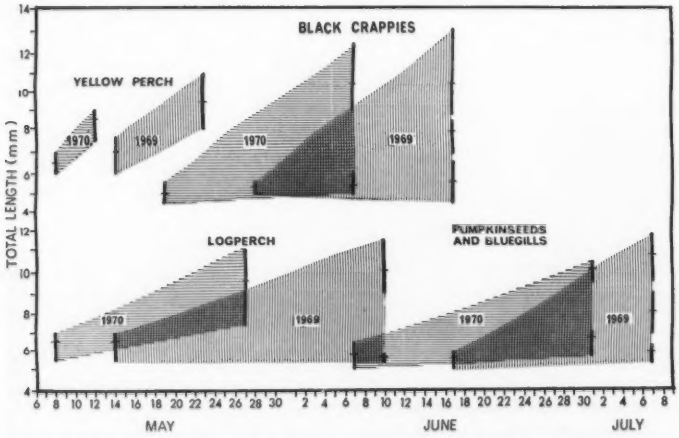

FIG. 4. Total lengths of free-swimming perciform larvae at first appearance and peak abundance. Vertical bars, lengths; short horizontal lines, means; shaded areas, extrapolated lengths.

those in previous studies and only the nesting sites of black crappies were not located in the nest-site area.

Acknowledgments — The present work, one of a series on the comparative ecology of larval fish, was partially supported by the National Research Council of Canada and we express our thanks to that body for its support. It was carried out at the Lake Opinicon Research Station of Queen's University and we thank the University and the Director of the Station, Prof S. R. Brown, for the use of these facilities.

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The Mud-Dwelling Hydrozoan *Boreohydra simplex* in the Western North Atlantic[1]

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CALDER, D. R. 1974. The mud-dwelling hydrozoan *Boreohydra simplex* in the western North Atlantic. J. Fish. Res. Board Can. 31: 1666–1667.

Boreohydra simplex was collected at a depth of 400 m in Cabot Strait, eastern Canada; this solitary, mud-dwelling hydroid is previously unreported from the western North Atlantic. Elsewhere, it has been found along the coasts of Scandinavia, Britain, and Iceland in the North Atlantic, and from South Georgia in the South Atlantic.

CALDER, D. R. 1974. The mud-dwelling hydrozoan *Boreohydra simplex* in the western North Atlantic. J. Fish. Res. Board Can. 31: 1666–1667.

Nous avons recueilli *Boreohydra simplex* à une profondeur de 400 m dans le détroit de Cabot, sur la côte est du Canada; cet hydroïde de vase, solitaire, n'avait jamais été signalé auparavant dans l'ouest de l'Atlantique-Nord. Ailleurs, on l'a trouvé le long des côtes de la Scandinavie, de l'Angleterre et de l'Islande en Atlantique Nord, et depuis la Georgie du Sud en Atlantique Sud.

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Borechydra simplex is a solitary marine hydroid belonging to the suborder Capitata. It has reduced oral tentacles, prominent knobs of nematocysts scattered over the hydranth, and a stem adapted for digging in a muddy substrate. The species lacks a medusa stage in its life history.

Boreohydra simplex was originally described by Westblad (1937) from the coast of Norway. Subsequent records indicate that it is relatively common along the western coast of Scandinavia (Hult 1941; Rees 1938, 1952; Westblad 1953). Elsewhere, it has been reported from Britain and Iceland in the North Atlantic, and from South Georgia in the South Atlantic (Westblad 1953). It is reported here from the western North Atlantic for the first time. The record is based on a single specimen found in a plankton sample taken during 1969 by the Gulf of St. Lawrence Project, International Biological Program. The hydroid was given to me for identification by personnel of the Canadian Oceanographic Identification Centre, National Museum of Natural Sciences, Ottawa. A brief account of the specimen is given here.

[1]Contribution No. 21 from the South Carolina Marine Resources Center, Charleston, S.C. 29412, USA.

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Boreohydra simplex Westblad 1937

FIG. 1.

Boreohydra simplex Westblad 1937, p. 1, figs. 1–4; Rees 1938, p. 37; Hult 1941, p. 455, figs. 1–3; Westblad 1947, p. 1, figs. 1–4; Ewer 1948, p. 233; Nyholm 1951, p. 531, figs. 1–4; Rees 1952, p. 5, 6; Westblad 1953, p. 351, fig. 1; Rees 1957, p. 507, 519, 522, fig. 52; Nyholm 1963, p. 289, fig. 1.

Material examined — One infertile specimen, Cabot Strait, 47°14′35″ N, 59°57′35″ W, 400 m, June 1, 1969. Cat. No. 790, National Museum of Natural Sciences, National Museums of Canada.

Description — Polyp solitary, with large batteries of nematocysts scattered over hydranth from its juncture with hydrocaulus to tentacles, hydranth vermiform, 1.5 mm long, maximum width 0.55 mm, oral tentacles three, reduced, capitate; hypostome dome-shaped. Hydrocaulus 1.2 mm long, slender, tapering gradually. Gonads lacking.

Remarks — The specimen of *B. simplex* was collected in a deep oblique plankton tow taken with a $\frac{1}{2}$-m net of No. 6 mesh (0.239-mm aperture size). The net apparently touched bottom because the sample contained polychaetes, cumaceans, and the isopod *Munnopsis*, as well as *Boreohydra*. The substrate in the area of collection, I. B. P. Station 2, Cabot Strait, was mostly mud with some

FIG. 1. *Boreohydra simplex* from Cabot Strait, Gulf of St. Lawrence.

sand and shell particles. Specimens of this species are likely to be encountered in benthic samples from similar substrates in the Gulf of St. Lawrence and adjacent areas.

The systematic position of *B. simplex* is uncertain. Initially, Westblad (1937) believed that it was related to the genus *Protohydra* Greeff 1870, but later (Westblad 1947) recognized its affinities with the Capitata and erected a new family, the Boreohydridae, for the species. Rees (1957) believed there was no justification for this new family, considering *B. simplex* to be an aberrant corymorphine. Histological studies are warranted to determine whether the scattered nematocyst batteries over the hydranth could be interpreted as vestigial tentacles. If so, the species may belong to the family Myriothelidae.

Acknowledgments — I am indebted to Mrs J. Fournier for bringing the specimen to my attention, and to Dr D. J. Faber for providing the relevant collection data.

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An Inexpensive Multiple Level Water Sampler

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GOODWIN, M. H., AND C. I. GODDARD. 1974. An inexpensive multiple level water sampler. J. Fish. Res. Board Can. 31: 1667–1668.

An inexpensive nonmetallic water sampler was designed to secure multiple samples simultaneously from different depths. The device is constructed of readily available materials and may be operated from a small boat.

GOODWIN, M. H., AND C. I. GODDARD. 1974. An inexpensive multiple level water sampler. J. Fish. Res. Board Can. 31: 1667–1668.

Un échantillonneur d'eau non métallique et peu dispendieux a été construit pour recueillir des échantillons simultanés à des niveaux différents. L'appareil est construit de matériaux faciles à obtenir, et on peut l'opérer d'un petit bateau.

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THIS is a description of an inexpensive multiple-bottle sampler designed for use in determining water column profiles. The sampler is constructed of readily available materials and may be operated by hand from a small boat. The usual practice of attaching a series of Nansen bottles to a hydrographic wire is difficult to carry out on small craft and is prohibitively expensive in small-scale investigations.

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The sample bottle is constructed from a 25-cm length of ABS (acrylonitrile-butadiene-styrene) drain pipe (5.3 cm inside diameter) to which a nylon rope bridle is attached with plastic tape (Fig. 1A). The bridle is mounted off center so that, when the unit is suspended, the pipe is held at a steep angle to the horizontal. Two rubber balls (7.5 cm diameter) are attached to a piece of amber laboratory tubing (6 mm outside diameter) passed through the pipe. The tubing is forced through the balls with the aid of long-nosed pliers and a brass ring is tied to each end of the tubing. Before tying, the tubing is stretched so that the balls will make a tight seal at the ends of the pipe.

The desired number of sample bottles are then attached to a 1-cm braided polypropylene line tied to a 25-kg weight (Fig. 1B). This is easily done by clipping the brass rings on the sampler bridle (Fig. 1A, a′) to brass rings tied to the weighted line. A minimum spacing of 30 cm is required between sample bottles. To prepare the units for sampling, the opposing balls are brought together at the midpoint of the pipe and the brass rings (Fig. 1A, a) tied together with a slip knot (Fig. 1C). All the pairs of balls are tied using the same 3-mm nylon line, so that, when the end of the trip line is pulled, all knots collapse in sequence and the balls seal the pipes. Very little line is required to form the slip knots and consequently as many as 20 sample bottles can be simultaneously tripped with one pull of the trip line.

In fields tests, we prepared the sampler and secured 20 samples of approximately 500 ml each from a site in less than 5 min. As the samples were used for salinity determinations, contamination with air was not a consideration. Since in no case did the balls fail to seal the pipe ends, we are confident that no air was retained in the samples.

A simple plastic valve may be cemented into an end of each pipe to permit the withdrawal of samples for dissolved oxygen determinations using a technique similar to that employed with conventional Van Dorn water samplers.

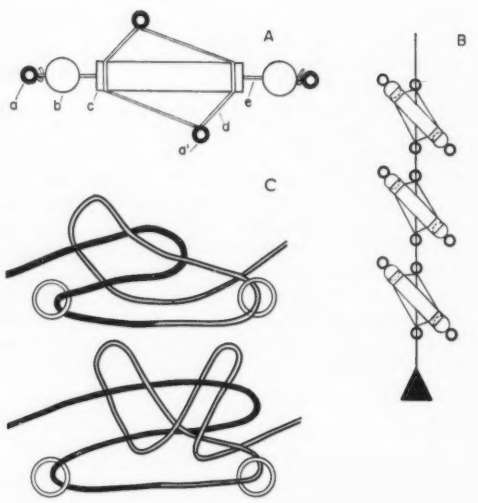

FIG. 1. A, construction details of a single sampler: a,a′, brass rings; b, rubber ball; c, ABS pipe; d, nylon rope bridle; e, amber laboratory tubing, passed through pipe and balls and tied to brass rings. B, three samplers arrayed on the weighted line, after samples have been taken. C, details of slip knot; solid portion of line extends to next sampler and open portion to surface for tripping the devices.

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Predator–Prey and Competition Models with State Variables: Biomass, Number of Individuals, and Average Individual Weight

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JENSEN, A. L. 1974. Predator–prey and competition models with state variables: biomass, number of individuals, and average individual weight. J. Fish. Res. Board Can. 31: 1669–1674.

Applying the identity that biomass equals number of individuals multiplied by average individual weight, simultaneous equations for change with respect to time in biomass, number of individuals, and average individual weight are obtained for Kostitzin's predator–prey equations and for the Lotka–Volterra competition equations. By the same procedure applied here, simultaneous equations for these three variables can be obtained for other predator–prey and competition equations These equations can be applied to determine the biomass, number of individuals, and average individual weight of interacting fish populations under different rates of exploitation.

JENSEN, A. L. 1974. Predator–prey and competition models with state variables: biomass, number of individuals, and average individual weight. J. Fish. Res. Board Can. 31: 1669–1674.

A partir du postulat que la biomasse est égale au nombre d'individus multiplié par leur poids moyen, on obtient des équations simultanées représentant les changements dans le temps de la biomasse, du nombre d'individus et du poids moyen des individus pour les équations prédateur–proie de Kostitzin et les équations de Lotka–Volterra relatives à la concurrence. Une procédure semblable, appliquée ici, permet de formuler des équations simultanées pour ces trois variables applicables à d'autres modèles prédateur–proie et concurrence. Ces équations peuvent servir à déterminer la biomasse, le nombre d'individus et le poids individuel moyen de populations de poissons agissant les unes sur les autres, lorsque celles-ci sont soumises à des taux d'exploitation différents.

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ALL species that are fished, live in close association with other species, and studies of interactions among fish species are important to fisheries management (Larkin 1963, 1966). Larkin (1956, 1963, and 1966) has applied predator–prey and competition models to determine the theoretical result of exploiting either or both of a pair of competing species and either or both of a predator–prey pair.

Application of the classical predator–prey and competition models to fisheries studies results in surplus production models for yield in which growth, reproduction, and natural mortality of the interacting species are all combined in a common expression. Larkin's studies were done using the number of individuals of each species as the vector of state. The decision to construct models for fish population interactions in terms of number of individuals rather than in terms of biomass is an important decision. Jensen (1972) has shown that because biomass, B, number of individuals, N, and average individual weight, $\bar{W}$, are related by the identity,

$$B(t) = N(t)\ \bar{W}(t), \qquad (1)$$

where t is time; independent models cannot be simultaneously constructed for these three variables. Jensen (1972) has derived simultaneous equations for biomass, number of individuals, and average individual weight implied by Schaefer's surplus production equation. He showed that if change with respect to time in biomass of a population is

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described by the logistic equation, then change in number of individuals with respect to time can be described by the logistic equation only if there is no change with respect to time in average individual weight or if change in number of individuals is independent of change in average individual weight. These are not realistic assumptions for fish populations.

In this note simultaneous equations for biomass, number of individuals, and average individual weight are developed for the Lotka (1956) and Volterra (1928) competition equations, and for Kostitzin's (1939) predator–prey equations. Larkin (1963) applied the Lotka–Volterra equations to study interspecific competition and exploitation, and Larkin (1966) applied Kostitzin's predator–prey equations to study exploitation in a predator–prey situation. Larkin (1966) concluded that Kostitzin's predator–prey equations are more realistic for fish populations than the Lotka–Volterra predator–prey equations. Fish prey on a variety of organisms and extinction of a single prey species may not lead to extinction of the fish population. In the Lotka–Volterra predator–prey model extinction of the predator results in exponential growth of the prey and extinction of the prey results in extinction of the predator. In Kostitzin's predator–prey equations the population density of the prey has an upper limit in the absence of the predator, and the population density of the predator has a lower limit in the absence of the prey. Kostitzin's predator–prey equations are nearly identical in mathematical form to the Lotka–Volterra competition equations. The method illustrated here to obtain equations for biomass, number of individuals, and average individual weight can be applied to obtain similar equations for other predator–prey and competition models.

Mathematical symbols are listed below; the first species is the prey species or the first of two competing species, and the second species is a predator species or the second of two competing species.

b_1, b_2 = coefficients of interaction between first and second species

B_1, B_2 = biomass of first and second species

F_1, F_2 = fishing mortality coefficients for biomass of first and second species

F_3, F_4 = fishing mortality coefficients for number of individuals of first and second species

F_5, F_6 = fishing mortality coefficients for average individual weight of first and second species

g_1, g_2 = coefficient of growth in average individual weight of first and second species

h_1, h_2 = coefficient of intraspecific interaction for first and second species

k_1 = coefficient of increase in number of individuals of first species

k_2 = coefficient of increase in number of individuals of second species in competition model and coefficient of mortality of predator in predator–prey model

N_1, N_2 = number of individuals of first and second species

p_1, p_2 = coefficients of intraspecific interaction for first and second species

q_1, q_2 = coefficients of interaction between first and second species

r_1 = coefficient of biomass increase of first species

r_2 = coefficient of biomass increase of second species in competition model and coefficient of negative feedback for biomass of predator in predator–prey model

u_1, u_2 = coefficient of interaction between first and second species

$\bar{W}_1$, $\bar{W}_2$ = average individual weight of first and second species

Relation among biomass, number of individuals, and average individual weight — Differentiation of equation (1) with respect to time gives the equation,

$$\frac{dB}{dt} = N\frac{d\bar{W}}{dt} + \bar{W}\frac{dN}{dt}. \qquad (2)$$

If equations are specified for $d\bar{W}/dt$ and dN/dt, the equation for dB/dt is implicitly specified by equation (2). If equations are constructed independently for both $d\bar{W}/dt$ and dN/dt, changes in average individual weight and number of individuals are independent. Such equations imply two independent upper limits — one that determines the maximum number of individuals and one that determines the maximum average individual weight (Jensen 1972). If an equation relating growth to environmental carrying capacity is constructed for biomass there is a single upper limit, termed the environmental carrying capacity. An equation with

a single upper limit and mutual dependence of number of individuals and average individual weight provides a more realistic description of fish populations than a model with two upper limits and mutual independence of average individual weight and number of individuals. Therefore, the Lotka–Volterra competition equations and Kostitzin's predator–prey equations are developed in terms of biomass; then mutually dependent equations, corresponding to the biomass equations, are developed for number of individuals and average individual weight.

The equations for change in number of individuals and the equations for change in average individual weight are not uniquely determined by equation (2) and the equation for biomass change. To develop equations for change in number of individuals and equations for change in average individual weight it is necessary to make additional assumptions. These assumptions concern: 1) the form of the equations for number of individuals, 2) the mutual dependence of average individual weight and number of individuals, and 3) the patterns of algebraic signs in the equations for change in average individual weight. Many different systems of simultaneous equations, which correspond to different assumptions, can be derived for biomass, number of individuals, and average individual weight. The systems of equations derived in this note are simple systems in which the mathematical form of the equations for dB/dt, dN/dt, and $d\overline{W}/dt$ are similar, $d\overline{W}/dt$ does not equal zero, and N_1, N_2, $\overline{W}_1$, and $\overline{W}_2$ are all interrelated.

It is noteworthy that the equations for dN/dt and dB/dt have been tested with empirical observations. The equations for $d\overline{W}/dt$ have not previously appeared in the literature, and these equations have not been tested with empirical observations. Although the form of the equations for $d\overline{W}/dt$ result from the form of the equations for dN/dt and dB/dt, the equations for $d\overline{W}/dt$ must be considered as untested hypotheses until they are tested with empirical observations.

Predator–prey and competition models have been applied interchangeably to biomass and number of individuals. Therefore, it appears reasonable when developing simultaneous equations for biomass, number of individuals, and average individual weight, to assume that the equations for change in number of individuals are of the same mathematical form as the equations for change in biomass. For change in average individual weight and change in number of individuals to be mutually dependent both the equation for change in number of individuals and the equation for change in average individual weight must contain terms for average individual weight and number of individuals. The above assumptions, together with equation (2), uniquely determine the equations for change in number of individuals. For example, if biomass is defined by the logistic equation, $dB/dt = a_1B - a_2B^2$, then, to be of the same mathematical form as the biomass equation, contain both number of individuals and average individual weight, and satisfy equation (2), the equation for change in number of individuals must be $dN/dt = b_1N - b_2N^2\overline{W}$.

When the equations for dB/dt and dN/dt are specified, the form of the equation for $d\overline{W}/dt$ is implicitly specified to within a narrow degree, and only a small amount of biological information is necessary to complete its specification. For example, if for the logistic equation biomass and number of individuals are described by the equations given above, to satisfy equation (2) average individual weight must be given by $d\overline{W}/dt = 0$, $d\overline{W}/dt = \pm c\overline{W}$, or $d\overline{W}/dt = \pm c_1\overline{W} \pm c_2\overline{W}^2N$. Only the last equation for $d\overline{W}/dt$ satisfies the condition that N and $\overline{W}$ are mutually dependent. It is biologically realistic to assume that input to average individual weight is proportional to average individual weight and that an increase in number of individuals results in a more intense intraspecific competition and a lower rate of change in average individual weight. Therefore, the equation for change in average individual weight is $d\overline{W}/dt = c_1\overline{W} - c_2\overline{W}^2N$.

Kostitzin's predator–prey equations — Under the assumptions: 1) the equations for change in number of individuals are of the same form as the equations for change in biomass, 2) the variables N_1, N_2, $\overline{W}_1$, and $\overline{W}_2$ are interrelated, and 3) selection of algebraic signs in the equations for change in average individual weight is correct, application of equation (2) shows that Kostitzin's predator–prey equations for change in biomass, number of individuals, and average individual weight are:

$$\begin{aligned}
dB_1/dt &= r_1B_1 - a_1B_1^2 - b_1B_1B_2 - F_1B_1\\
dB_2/dt &= -r_2B_2 - a_2B_2^2 + b_2B_1B_2 - F_2B_2\\
dN_1/dt &= k_1N_1 - p_1B_1N_1 - q_1N_1B_2 - F_3N_1\\
dN_2/dt &= -k_2N_2 - p_2N_2B_2 + q_2N_2B_1 - F_4N_2\\
d\overline{W}_1/dt &= g_1\overline{W}_1 - h_1\overline{W}_1B_1 \pm u_1\overline{W}_1B_2 - F_5\overline{W}_1\\
d\overline{W}_2/dt &= g_2\overline{W}_2 + u_2\overline{W}_2B_1 - h_2\overline{W}_2B_2 - F_6\overline{W}_2.
\end{aligned} \qquad (3)$$

The constants are related by the equations: $r_1 = k_1 + g_1$, $r_2 = k_2 - g_2$, $a_1 = p_1 + h_1$, $a_2 = p_2 + h_2$, $b_1 = q_1 \pm u_1$, $b_2 = q_2 + u_2$, $F_1 = F_3 + F_5$, and $F_2 = F_4 + F_6$. Under equilibrium conditions, where all of the derivatives are zero, solution of

equations (3) for B_1 shows the following additional constraints on the constants,

$$\frac{F_1 - r_1 + b_1B_2}{-a_1} = \frac{F_2 + r_2 + a_2B_2}{b_2} = \frac{F_3 - k_1 + q_1B_2}{-p_1} =$$

$$\frac{F_4 + k_2 + p_2B_2}{-q_2} = \frac{F_5 - q_1 \pm u_1B_2}{-h_1} = \frac{F_6 - g_2 + h_2B_2}{u_2},$$

where $B_2 = (-r_2a_1 - b_2F_1 + r_1b_2 - F_2a_1)/(a_1a_2 + b_1b_2)$.

In equations (3), the biomass equations are identical to the equations obtained when Kostitzin's predator–prey equations are applied to biomass alone. But the equations for change in number of individuals are different from the equations that would be obtained if Kostitzin's equations had been applied to number of individuals alone. Both the equation for change in number of prey and the equation for change in number of predators contain terms for prey biomass and predator biomass.

In the equation for change in number of prey, the birth rate of the prey is proportional to the number of prey. Mortality of the prey depends on both the product of the number of prey with prey biomass and the product of the number of prey with predator biomass.

In the equation for change in number of predators, the birth rate of the predator depends on the product of the number of predators with prey biomass. Mortality of the predator depends both on the number of predators and the product of the number of predators with predator biomass.

These equations for change in number of prey and for change in number of predators are biologically realistic. Birth rate of the prey is proportional to the number of prey. Mortality of the prey increases with either an increase in the number of prey or with an increase in prey biomass. Higher prey biomass and a larger prey population density both result in more intense intraspecific competition. Mortality of the prey also increases with predator biomass. A larger predator biomass requires a larger amount of food.

For both natural and experimental fish populations it has been established that average individual weight is related to the number of individuals (Nikolskii 1969; Swingle and Smith 1941). And the carrying capacity of an environment for fish appears to be related to the biomass of the fish population rather than to the number of individuals (Swingle and Smith 1941). Equations for change in number of individuals that are a function of biomass as well as a function of number of individuals are, therefore, more complete and realistic than equations that do not contain terms for biomass.

If Kostitzin's equations had been applied to number of individuals alone, mortality of the prey would have been a function of neither predator biomass nor prey biomass. But if average individual weight of the predator and prey are not constant, the number of prey does not accurately determine the amount of food the prey supply the predator and the number of predators does not accurately determine the food requirements of the predators.

In equations (3), the equations for both biomass and number of individuals are similar to the equations obtained when Kostitzin's equations are applied to each of these variables alone, and the equations for each variable alone have been thoroughly investigated both biologically (Gause 1964) and mathematically (Goel et al. 1971). Equations for change in average individual weight of a predator and its prey have not been previously proposed, and they must be considered more carefully than the equations for change in biomass and number of individuals.

The equations for change in average individual weight cannot be developed independently of the equations for biomass and number of individuals. The equations for change in average individual weight are developed by: 1) specifying the equations for change in biomass and the equations for number of individuals, 2) the requirement that the variables be mutually dependent, and 3) selection of algebraic signs based on biological assumptions.

The mathematical form of the equations for change in average individual weight is the same as the mathematical form of the equations for biomass and number of individuals, but the algebraic signs are different. Equations (3) indicate that an increase in the prey biomass results in more intense intraspecific competition and a slower change in average individual weight of prey. The equation for change in average individual weight of the prey also contains the term $\pm u_1\overline{W}_1B_2$. The sign of this term is positive if predators select larger prey, the sign is negative if predators select smaller prey, and this term is zero if on the average predators select all size-groups of prey equally often.

Change in average individual weight of the predator depends on both average individual weight of the predator and the product of average individual weight of the predator with biomass of prey; this second term realistically indicates that change in average individual weight of the predator depends on the biomass of food available. Loss in average individual weight of the predator depends on the product of the average individual weight of the predator with predator biomass. This term realistically indicates that as predator biomass increases,

intraspecific competition increases and change in average individual weight decreases.

Lotka–Volterra competition equations — Under the assumptions applied to obtain equations (3), application of equation (2) shows that the Lotka–Volterra competition equations for change in biomass, number of individuals, and average individual weight are:

$$\begin{aligned}
dB_1/dt &= r_1B_1 - a_1B_1^2 - b_1B_1B_2 - F_1B_1 \\
dB_2/dt &= r_2B_2 - a_2B_2^2 - b_2B_1B_2 - F_2B_2 \\
dN_1/dt &= k_1N_1 - p_1B_1N_1 - q_1N_1B_2 - F_3N_1 \\
dN_2/dt &= k_2N_2 - p_2N_2B_2 - q_2N_2B_1 - F_4N_2 \\
d\overline{W}_1/dt &= g_1\overline{W}_1 - h_1\overline{W}_1B_1 - u_1\overline{W}_1B_2 - F_5\overline{W}_1 \\
d\overline{W}_2/dt &= g_2\overline{W}_2 - h_2\overline{W}_2B_2 - u_2\overline{W}_2B_1 - F_6\overline{W}_2.
\end{aligned} \tag{4}$$

The constants are related by the equations: $r_1 = k_1 + g_1$, $r_2 = k_2 + g_2$, $a_1 = p_1 + h_1$, $a_2 = p_2 + h_2$, $b_1 = q_1 + u_1$, $b_2 = q_2 + u_2$, $F_1 = F_3 + F_5$, and $F_2 = F_4 + F_6$. Under equilibrium conditions, where all of the derivatives are zero, solution of equations (4) for B_1 shows restrictions on the constants of equations (4) similar to those obtained for equations (3).

In equations (4), the equations for change in biomass are identical to the equations obtained when the Lotka–Volterra competition equations are applied to biomass alone. The equations for change in number of individuals and the equations for change in average individual weight are different from the equations that would be obtained by application of the Lotka–Volterra competition equations to either variable alone.

The equation for change in population density of the first species contains the intraspecific competition term $p_1B_1N_1$ and the equation for change in population density of the second species contains the intraspecific competition term $p_2B_2N_2$. These terms indicate that the intensity of intraspecific competition depends on both the number of individuals and the biomass of the species. The equations for change in population density of the first species contains the interspecific competition term $q_1N_1B_2$ and the equation for change in population density of the second species contains the interspecific competition term $q_2N_2B_1$. These terms indicate that the intensity of interspecific competition depends on the number of individuals of the species and on the biomass of the competing species.

In equations (4), the change in average individual weight of both competing species is proportional to their average individual weight. Loss in average individual weight of each species depends on the biomass of both species; as the biomass of both species increases, both intraspecific and interspecific competition increase. Equations (4) are more realistic for fish populations than the equations obtained when the Lotka–Volterra equations are applied to number of individuals alone. Changes in number of individuals are related to population biomass. Equations (4) contain terms for biomass, whereas equations obtained when the Lotka–Volterra model is applied to number of individuals alone do not contain terms for biomass.

Discussion — Relations among biomass, number of individuals, and average individual weight are important in fisheries biology. For fish populations the environmental carrying capacity is the maximum biomass that the environment can sustain, and the same resources can support large populations of small fish or small populations of large fish of the same species (Nikolskii 1969; Swingle and Smith 1941). Fishing a population decreases the number of fish and, by selection of older and larger individuals, decreases the average individual weight. Expanding surplus production models to include number of individuals and average individual weight as well as biomass may, therefore, increase the usefulness of these models for fisheries management.

The expanded models can be applied to determine number of individuals, biomass, and average individual weight for predator–prey and competing species that result from different exploitation rates. For example, for Kostitzin's predator–prey model at equilibrium under average environmental conditions,

$$B_1 = \frac{F_1a_1a_2 - r_1a_1a_2 - r_2a_1b_1 - a_1b_1F_2}{-a_1(a_1a_2 + b_1b_2)}$$

$$B_2 = \frac{b_2r_1 - r_2a_1 - b_2F_1 - a_1F_2}{a_1a_2 + b_1b_2}$$

$$N_1 = \frac{F_1a_1a_2 - r_1a_1a_2 - r_2a_1b_1 - a_1b_1F_2}{-a_1\overline{W}_1(a_1a_2 + b_1b_2)}$$

$$N_2 = \frac{b_2r_1 - r_2a_1 - b_2F_1 - a_1F_2}{\overline{W}_2(a_1a_2 + b_1b_2)}$$

$$\overline{W}_1 = \frac{F_1a_1a_2 - r_1a_1a_2 - r_2a_1b_1 - a_1b_1F_2}{-a_1N_1(a_1a_2 + b_1b_2)}$$

$$\overline{W}_2 = \frac{b_2r_1 - r_2a_1 - b_2F_1 - a_1F_2}{N_2(a_1a_2 + b_1b_2)}$$

The above equations are as easily applied as the surplus production equations for biomass alone, but data are needed for number of individuals and average individual weight as well as for biomass.

Accurate estimation of the constants in equations (3) and (4) is difficult. A linearization and curve fitting procedure similar to the one applied by Schaefer (1957) to estimate the constants in the Schaefer surplus-production model can be applied to estimate the constants in equations (3) and (4). The equations are linearized by estimation of the derivatives with the two point formula (Schaefer 1957; Hamming 1962). Schaefer's method of data partition does not produce unique estimates of the constants (Pella and Tomlinson 1969). Least squares can be applied to the linearized equations to estimate the constants as illustrated by Pella and Tomlinson (1969). The two point formula for linearization results in underestimation of the derivative (Hamming 1962; Pella and Tomlinson 1969) and as a general rule numerical integration should be applied instead of numerical differentiation whenever possible (Hamming 1962). Pella and Tomlinson (1969) have developed a method for approximation of the general surplus-production model in which numerical integration is applied instead of numerical differentiation. Equations (2) and (3) cannot, however, be solved in closed form and the method of Pella and Tomlinson cannot be applied.

In summary, biomass, number of individuals, and average individual weight are mutually dependent variables. For most fish populations the environmental carrying capacity is the maximum biomass sustainable by the environment rather than the maximum number of individuals. Population models for fish should, therefore, be constructed in terms of biomass or in terms of biomass and number of individuals. Surplus production models that are constructed for number of individuals alone are not more easily constructed than models for biomass alone, and they ignore the interrelations among average individual weight, biomass, and number of individuals.

Data for application of competition and predator–prey equations to natural or experimental fish populations do not appear to exist. This lack of data limits application of models for interactions of exploited fish populations to theoretical considerations such as those of Larkin (1956, 1963, and 1966). Continued development of models for interaction among species is necessary for theoretical studies, and the models can also serve as guides for the design of studies on experimental and natural fish populations.

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Feeding Efficiencies of the Polychaete *Nereis virens* Cultured on Hard-Clam Tissue and Oyster Detritus[1]

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TENORE, K. R., AND U. K. GOPALAN. 1974. Feeding efficiencies of the polychaete *Nereis virens* cultured on hard-clam tissue and oyster detritus. J. Fish. Res. Board Can. 31: 1675–1678.

In laboratory experiments, the ecological and assimilation efficiencies of the polychaete *Nereis virens* cultured on biodeposits of oysters (5.7 and 28.8%) were lower than for worms grown on clam tissue (18.0 and 77.3%). However, a high consumption rate of biodeposits resulted in a growth rate (48% increase in dry wt) higher than for worms fed clam tissue (31% increase). Mucus production by *Nereis virens* accounted for several percentage points in the calculation of efficiencies. Biodeposits in both natural and aquaculture environments might be exploited as a food source for this species.

TENORE, K. R., AND U. K. GOPALAN. 1974. Feeding efficiencies of the polychaete *Nereis virens* cultured on hard-clam tissue and oyster detritus. J. Fish. Res. Board Can. 31: 1675–1678.

Au cours d'expériences de laboratoire, l'efficacité écologique et celle d'assimilation du polychète *Nereis virens* nourri de biodépôts d'huître (5.7 et 28.8%) ont été plus basses que celles de vers élevés au tissu de coque (18.0 and 77.3%). Cependant, un taux élevé de consommation des biodépôts a entraîné un rythme de croissance plus élevé (augmentation de 48% en poids sec) que celui des vers nourris de tissu de coque (augmentation de 31%). La production de mucus par *Nereis virens* rend compte de plusieurs points en pourcentage dans le calcul des efficacités. Les biodépôts, tant dans les milieux naturels que dans ceux d'aquiculture, pourraient être exploités comme source de nourriture pour cette espèce.

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INFORMATION on the nutritive value of detritus to facultative detrital feeders such as *Nereis virens* (Sanders 1962, Clark 1962) would be valuable in elucidating the importance of detritus in marine food chains. Darnell (1967) pointed out that most reports only imply the significance of detritus in marine food chains and little critical or quantitative research on rates of utilization on food chain efficiencies is available. Therefore we compared growth rates and feeding efficiencies of the clam worm *N. virens* cultured on biodeposits of the oyster *Crassostrea virginica* and on tissue of the hard clam *Mercenaria mercenaria*.

Materials and methods — Oysters (4–6 cm in length) obtained from Flower Brother and Sons, Bayville, Long Island were cultured in fiberglass trays (57 × 40 × 10 cm) that received 1 μ-filtered sea water with temperature regulated to 20 ± 1 C (Tenore and Huguenin 1973). Each tray contained 50 oysters and was continuously supplied with a culture of mixed species of phytoplankton dominated by *Phaeodactylum tricornutum*. Biodeposits were siphoned out from the trays into a beaker and the trays cleaned every 5 days. After centrifugation the deposits were placed on filter paper, allowed to air dry, and then made into pellets about 2 mm in diameter and frozen until used. Meat of *Mercenaria mercenaria* was minced and also frozen.

Worms originally collected in Maine were obtained from a local bait dealer and held in tanks containing sand and seaweed and receiving ambient-temperature sea water.

Wet and dry weights (90 C for 24 h) of samples of both new and uneaten food, fecal material, mucus, and tissue of the worms were also determined. The carbon and nitrogen contents (%) of these materials were also measured with a Perkin-Elmer Model 240 Elemental Analyzer. The carbon compositions were used to con-

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vert the dry weights obtained during the experiment into organic carbon values and to calculate and compare the ecological and assimilation efficiencies of the worms fed on the two foods. The gross ecological efficiency, i.e. net production (growth)/food ingested, was calculated both by not including and by including mucus production. The assimilation efficiency (net production/food assimilated) was calculated including mucus production.

The carbon and nitrogen contents (%) of the various materials were: tissue of *N. virens*, 45.7, 11.8; mucus of *N. virens*, 27.7, 6.1; biodeposits, 25.5, 4.3; clam tissue, 41.7, 9.7; and fecal material of *N. virens* fed on biodeposits, 16.9, 1.7, and on clam tissue, 32.2, 6.5.

In addition, food was withheld from cultures of worms to measure changes in weight and mucus production under starvation conditions.

All experiments were carried out in aerated polyethylene tanks (32 × 28 × 13 cm deep) containing 9 liters of 1 μ-filtered sea water. Clean pebbles were provided on the bottoms of the culture tanks and the cultures were covered during the experiment. For both the starvation and biodeposit experiments we had five replicate culture tanks (four replicates for clam tissue) each containing from two to four worms. Young worms ranging in size from 7–15 cm were held at the experimental temperature (20 ± 1 C) for about a week, feeding on the respective food source. The worms were then deprived of food for 24 h before initiation of the experiment.

During the 6 wk of the experiments each tank was cleaned every day by siphoning out and collecting the uneaten food and fecal material. New food was then introduced in sufficient quantities to ensure against food limitation effects. The culture water was replaced every other day. Wet weight of the worms was measured each week and dry weight estimated from a conversion factor (14.8%). Prior to weighing, the worms were removed from the experimental tanks and allowed to empty their alimentary tracts for 4–5 h in filtered aerated sea water.

Results — The average consumption of biodeposits was 1.720 g/g dry worms compared with 0.285 g of clam tissue (Table 1). The mean dry weight of worms fed biodeposits rose in 42 days from 0.455 to 0.674 g, an increase of 48%, and of those on clam tissue from 0.455 to 0.598 g, an increase of 31%.

Nereis virens produced an average of 0.01 g dry weight of mucus material/wk per gram dry worm.

Without including mucus production, the ecological efficiency for worms fed on biodeposits was 5.7% compared with 18.0% for worms cultured on clam tissue (Table 2). Including mucus production, the respective values rose to 7.0 and 22.9%. The assimilation efficiency including mucus production, was 28.8% for worms fed on biodeposits in contrast to 77.3% for worms on clam tissue.

Discussion — Although the constant decrease in the average feeding rate of the worms cultured on biodeposits might suggest adverse culture or food conditions, the growth rates of the worms compare favorably with those in nature. The biodeposits were formed into artificial pellets for the sake of handling and recovery. Although much surface detritus of benthic environments is in the form of fecal pellets, the larger size range of the experimental food might have adversely affected feeding rate. Similarly, the lower feeding and concomitant growth rates of the worms fed on clam tissue might also

TABLE 1. Weights at weekly intervals of *Nereis virens* fed on biodeposits of oysters (11–13 worms in five replicates) and on clam tissue (nine worms in four replicates) and mucus production of worms deprived of food. All values (grams) are given in dry weight.

	Worms fed deposits			Worms fed clam tissue			Worms not fed	
Time (*days*)	Total food consumed	Food consumed/ g worm[a]	Mean wt of worm	Total food consumed	Food consumed/ g worm[a]	Mean wt of worm	Total wt	Total mucus production
0	–	–	0.4549	–	–	0.4550	8.58	–
7	13.23	2.051	0.5073	1.136	0.271	0.4940	7.90	0.0487
14	12.79	1.890	0.5340	1.353	0.313	0.5100	7.38	0.0659
21	12.94	1.797	0.5740	1.340	0.301	0.5204	7.00	0.0728
28	10.56	1.624	0.6086	1.433	0.304	0.5474	6.57	0.0902
35	10.91	1.586	0.6425	1.347	0.280	0.5761	6.36	0.0590
42	9.92	1.370	0.6738	1.233	0.240	0.5976	6.18	0.0592
Total	70.35	10.32		7.842	1.71			0.3956

[a]On basis of average of mean weights of worms on test date and preceding date.

TABLE 2. Calculated efficiencies for *N. virens* fed on biodeposits of oysters and clam tissue. All biomass values are in grams carbon.

	13 worms fed biodeposits	9 worms fed clam tissue
Total food ingested	17.93	3.27
Total growth	1.03	0.59
Total mucus production	0.23	0.16
Egested feces	13.55	2.32
Assimilated carbon (ingested-egested)	14.38	0.97
Ecological efficiency (%) $\left(\frac{\text{net production}}{\text{food ingested}}\right)$		
mucus production excluded	5.7	18.0
mucus production included	7.0	22.9
Assimilation efficiency (%) $\left(\frac{\text{net production}}{\text{food assimliated}}\right)$		
mucus production included	28.8	77.3

reflect a feeding response to an uncommon food source. However, Bass and Braffield (1972) reported a wet weight increase per year of 3–7 g for *N. virens* in the Thames estuary. These data average about 0.096 g increase in wet weight per week, in comparison with 0.159 g for the worms fed on clam tissue and 0.243 g for those on the biodeposits. Even though the present data were obtained at 20 C whereas Bass and Braffield's data were averaged through a yearly temperature regime, the comparison suggests that the experimental worms had favorable culture conditions.

The carbon and nitrogen determinations and efficiency calculations indicate differences in response to the food sources of biodeposits and clam tissue. Although the worms ingested less total weight of clam tissue than of biodeposits, the higher ecological efficiency for these worms suggested that clam tissue was a more nutritive food source. In contrast, the lower nutritive quality of the biodeposits, as evidenced by the lower percent carbon and nitrogen, would require a higher feeding rate to satisfy nutritional requirements. The higher ecological efficiency of the worms feeding on clam tissue might be explained by their high assimilation efficiency. These worms assimilated more than 3 times as much food as those feeding on biodeposits.

However, even at the lower ecological and assimilation efficiencies, the biodeposits provided an adequate nutritional source for *N. virens*. The C:N ratio for the oyster biodeposits was 5.9:1, a ratio well below the 17:1 ratio suggested by Russel-Hunter (1972) as the highest ratio necessary for adequate nutritional requirements for most animals.

The possibility of these biodeposits being a food source for polychaetes is significant because of the enormous quantities of detritus available in coastal environments. In addition, the detritus usually has an associated micro- and meio-fauna that in itself could provide significant quantities of more nutritive organic matter to the polychaete. Radiotracer experiments (by K. R. Tenore unpublished data) suggest that the presence of meiofaunal species such as nematodes tremendously increase the incorporation rate of detritus by *N. virens*. Meiofaunal species were not present in the present experiment and so the present values might reflect base levels of nutrition in a detrital food chain for *N. virens*.

Work on polyaquaculture systems at Woods Hole has pointed out the possibility of culturing detrital feeding species on deposits of herbivore bivalves (Ryther et al. 1972; Tenore et al. 1973). The present data suggest that the commercially valuable bait worm *N. virens* is a possible species for such a polyculture system.

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Effect of Constant Temperature on Growth Rates of Pumpkinseed Sunfish (*Lepomis gibbosus*)[1]

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PESSAH, E., AND P. M. POWLES. 1974. Effect of constant temperature on growth rates of pumpkinseed sunfish (*Lepomis gibbosus*). J. Fish. Res. Board Can. 31: 1678–1682.

Relative growth rates of fall-captured *Lepomis gibbosus* exposed to six constant temperature regimes (5–30 C) were clearly separable for the first 6 wk. Thereafter, growth declined, becoming uniform between 15 and 30 C, and linear and negative at 10 and 5 C, respectively. A growth model between 15 and 30 C emerged as follows: 0–4 wk, rapid; 5–10 wk, intermediate; 11–16 wk, low uniform. The initial high followed by the low uniform stanza suggests "growth acclimation" took place.

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Les taux de croissance relative des *Lepomis gibbosus* capturés en automne et exposés à six régimes de température constante (5–30 C) sont clairement distinguables durant les 6 premières semaines. Par la suite, la croissance ralentit, est uniforme entre 15 et 30 C, linéaire et négative à 10 et 5 C respectivement. Un modèle de la croissance entre 15 et 30 C se présente comme suit: 0–4 semaines, rapide; 5–10 semaines, intermédiaire; 11–16 semaines, lente et uniforme. La phase du haut initial suivi d'un bas uniforme donne à croire qu'il y a «acclimatation de croissance».

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GROWTH rates in fish generally increase with increasing temperature to a maximum, then decline (Brown 1957). Bioenergetics studies in growth have shown that *Cichlasoma bimaculatum* (Warren and Davis 1967), for example, held for 14 days and fed ad lib., showed maximum growth at 28 C and minimal growth at 20 and 36 C for the period of observation. Several other workers have shown that there are also inherent "season-specific" growth rates (Saunders and Henderson 1969; and Gerking 1966) controlled by growth hormone output, and independent of temperature.

This study was primarily designed to test the limits of temperature-induced changes within the natural seasonal growth rate pattern of *Lepomis*

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gibbosus, which could be related to aquaculture and thermal pollution studies. Specific aspects concerning "growth acclimation" have not been reported for *Lepomis*, and may apply to other species if the observation period is sufficiently long.

Materials and methods — Pumpkinseed sunfish were seined from Lake-on-the-Mountain (97 ha), near Picton, Ontario. Dates of capture and corresponding surface water temperatures were: November 22, 1966, 7 C (Experiment 1); October 28, 1967, 12 C (Experiment 2). Fish were kept in a large holding tank at 12-h photoperiod and ambient water temperature for 2 days, and then transferred to experimental 100-liter tanks supplied with dechlorinated tap water through iron and P.V.C. pipe. Four fish of different sizes (e.g. 17–40 g) were selected for each experimental tank so that individual growth rates could be monitored without using tags. Measurements were accurate to within 0.4 g for wet weight.

The fish were fed small commercial oligochaetes at 4% wet body weight/day during holding and acclimation periods. Ad libitum feeding began 3 (Experiment 1) and 9 days (Experiment 2) prior to commencement of formal data aquisition. Acclimation was at a rate of 1 degree/day rise or 3 days/degree drop in temperature. Water temperatures were raised by 5- or lowered by 2-degree increments. Experiment 1 lasted 15 wk and experiment 2 was maintained for 30 wk, with data acquisition starting at day 30 and day 7, respectively, following acclimation.

The first experiment was conducted in one tank each at 5, 10, 20, 25, and 30 (±1) C and two tanks at 15 (±1) C. Limited facilities necessitated varied water flow rates of between 4.0 liters/min at 5 C and 0.4 liters/min at 30 C to maintain the desired temperatures. The second series of experiments was set up with replicate tanks at 15 and 25 (±1) C but constant flow rate at a 3.8 liters/min (the same flow rate used for 15 and 25 C in the first experiment). After 15 wk (Experiment 2) the water temperature in tanks at 15 C was raised to 25 C at a rate of 1 C/day and at 1-degree increments. Water temperature was kept at 25 (±1) C thereafter, until week 30.

Relative growth rates, h (Ricker 1958) were used to compare changes in growth between individuals and groups and were determined as follows:

$$h = \frac{\text{weight change for specific time period}}{\text{initial weight at beginning of the time period}} \times 100$$

Results — Experiment 1 — The initial versus final weights of fish (Table 1) over the 15-wk period fanned out in the classical pattern by temperature regimes. Thus the total growth increment over 15 wk varied from 0.98 at 5 C to 3.14 at 30 C, the maximum. Growth rates within the first 4 wk were much higher than for the remainder of the test period for fish held in temperatures 15 C and over. (In the case of the 25 C fish, this period of rapid growth extended to 7 wk.) From weeks 7 to 15, the relative growth rates declined to a much lower level.

The trends in growth were more clearly seen when plotted as in Fig. 1, and showed a similar pattern for temperatures 15–30 C. An early period of rapid growth tapered off to an even but slower rate past about week 5. The growth rate at 10 C was linear throughout the 15 weeks, but was very slow. There

TABLE 1. Initial and final mean weights of *Lepomis gibbosus* together with relative growth rates at six constant temperatures over 15 wk following acclimation.

		Temp (C)					
		5	10	15	20	25	30
	Weeks						
Relative growth rate (h value)	0–2	1.8	2.9	7.4	13.8	28.3	35.9
	3–5	–0.1	1.5	4.2	8.3	8.1	8.2
	5–7	–0.2	2.2	3.0	5.1	11.7	6.3
	7–9	–1.1	1.6	2.6	2.4	3.0	5.3
	9–11	1.3	1.6	2.6	2.2	2.8	2.9
	11–13	–0.6	0.6	2.2	2.6	3.0	4.0
	13–15	0.3	1.4	3.5	3.5	4.2	3.6
No. of fish	4	4	4	8	4	4	4
Mean initial wt (g)		34.6	34.6	35.4	31.9	30.5	24.2
Mean final wt (g)		35.2	43.6	58.3	68.1	84.2	76.1
Biomass accumulation		0.98	1.26	1.64	2.13	2.76	3.14

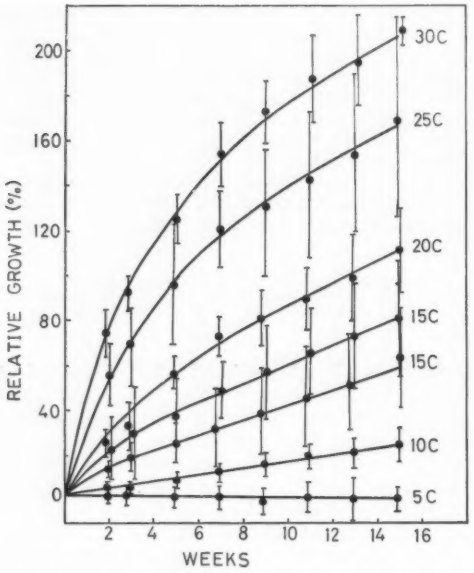

FIG. 1. Cumulative relative growth rates and 95% confidence limits for pumpkinseed sunfish (*Lepomis gibbosus*) kept at six constant temperatures over a 15-wk period and ad lib. feeding.

was no growth at 5 C, but some fluctuation above and below zero occurred.

Relative growth rates of fish during the first month were twice as great at 15 C and 6½ times as great at 30 C than they were for the same temperatures during the last month. Finally, the slopes for relative growth rates during weeks 12–15 (Fig. 2) for temperatures 15–30 C were not significantly different ($P = .05$). They fell within the range 11.8 ± 1.7 growth increments per 2-wk period for the final 12–15-wk period.

Experiment 2 — Similar patterns were observed during the second experiment, with "over-compensatory" growth following acclimation to both 15 and 25 C. There followed a period of reduced growth, and then a period of uniform growth rate of 5–6% for both series (Fig. 3) after 10 wk.

Raising the water temperature from 15 to 25 C after 16 wk resulted in another spike or "over-compensatory" growth period of from 9 to 14%/week for 6 wk, after which the growth rate again declined to the levels previously established at 15 C.

When results were combined and examined in terms of food uptake, the same trends became clear (Fig. 4). The curve for the first month (weeks 0–4) showed a much higher weekly ration than the total period (week 0–15). For weeks 5–9, food uptake rates were almost equal for temperatures 20, 25, and 30 C. During the last month, ration levels were further reduced. The level of food uptake, therefore, declined with time after an initial peak, as did relative growth rate.

Discussion and conclusions — The data presented here, if viewed on a cumulative basis, are in agreement with the literature in that total biomass produced for the total time period varied directly with temperature (e.g. Marcus 1932; Pentelow 1939; Brown 1957; Anderson 1959; Andrews and Stickney 1972). However, biweekly analyses showed that after an initial high following acclimation to higher temperature, relative growth rate differences between various temperatures above 15 C tended to be reduced with time. This "growth acclimation" or growth stabilization occurred at 15 C and above.

One puzzling aspect of the first experiment was the higher "initial" growth rate, as compared to

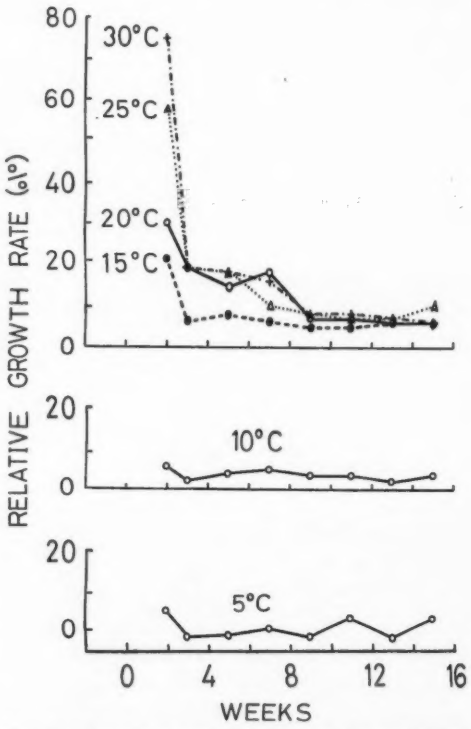

FIG. 2. Average relative growth rates of pumpkinseed over 15 wk, Experiment 1, at six constant temperatures.

the second experiment. Fish for Experiment 1 were acclimated for 5 wk longer than for Experiment 2. However, these fish were taken from 7-C waters, whereas the fish of Experiment 2 were taken at 12 C, which suggests that a longer acclimation time might have been necessary for fish taken from the cooler waters. Also, a temperature-induced growth spurt might be more pronounced in November fish. Kaya and Hasler (1972) state that either low temperature (10 C) or low photoperiod (below 10 h) will inhibit gametogenesis (= growth commencement) in the green sunfish *Lepomis cyanellus*. The change to 12 h and elevated temperatures did not start or stimulate gametogenesis in our fish, however, as gonads were later examined.

Kaya and Hasler's study (1972), however, suggests that photoperiods do not have to increase for the cycle to continue, but rather that anything over 15–16 h is necessary for commencement of the gonad cycle and growth of winter fish. Our fish had only 12 h, which is below this minimum. Perhaps the change was enough to cause a "false start" to the spring growth cycle, but daylight did not last sufficiently long for it to continue.

Coincident with the higher "initial growth" of fish in Experiment 1 was the time of commencement of ad lib. feeding, i.e. 3 days prior to the first experiment compared to 9 days for the second experiment. If the fish were truly temperature acclimated in each experiment, then perhaps one could consider a change in feeding regime (from 4% to ad lib.) as an activity stimulus. Initial rapid growth could thus have been attributable to the increase in ration rather than simply to temperature. Thus the change in food regime may have been an artifact within the true temperature–growth response. The greater initial growth rates at higher temperatures within each experiment may have also led to a broader "scope for activity" (Fry 1947) or S.D.A. (specific dynamic action, Warren and Davis 1967) from elevated temperature inducement of more active metabolic rates at the higher temperatures.

The data for lower temperatures (5 and 10 C) appeared to be consistent with field observations of Breder (1936). He observed that at temperatures below 10 C the species becomes quiescent. At 10 C our fish grew only 3%/2 wk and at 5 C no growth was recorded.

The most significant aspect presented here is the trend for fish between 15 and 30 C to level off in time to the same relative growth. Results were confirmed by experiment when a second elevation

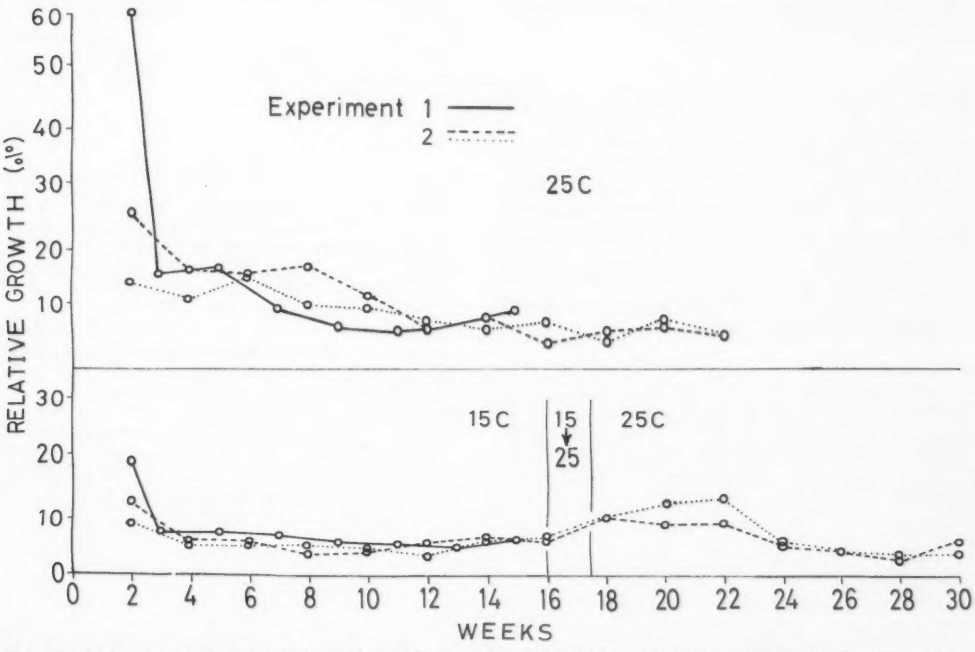

FIG. 3. Relative growth rates of pumpkinseed in Experiment 2, at two constant temperatures and constant flow rate. At week 16, the water temperature of the 15-C tank was raised to 25 C and maintained there.

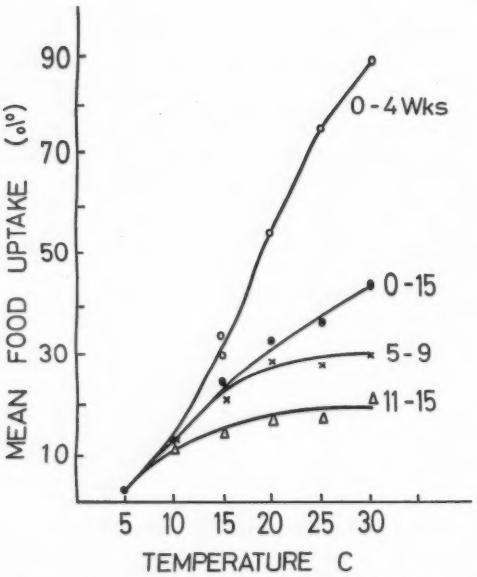

FIG. 4. Average relative food uptake rates (% body weight) at six constant temperatures for Experiment 1, fitted by eye, and divided into four periods. The pumpkinseed were fed ad lib. rations.

in temperature at week 16 caused a secondary "initial growth" spurt, followed subsequently by growth reduction to previously established 15-C level. Many other factors like food boredom, photoperiod, buildup of metabolites, and hierarchy, were all duly considered and discarded as contributory causes of the observed patterns (Pessah 1968). It would appear that *L. gibbosus* achieved full acclimation in terms of growth rate to constant temperatures from 15 to 30 C, with a standard level of growth the eventual result.

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PERSPECTIVES

Planned Transdisciplinary Approaches: Renewable Resources and the Natural Environment, Particularly Fisheries

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Abstract

REGIER, H. A., P. L. BISHOP, AND D. J. RAPPORT. 1974. Planned transdisciplinary approaches: renewable resources and the natural environment, particularly fisheries. J. Fish. Res. Board Can. 31: 1683–1703.

Ecologists who have long sought a larger role for their science and insights in the decision-making process now find that possibility open to them. But the recognition is dawning that traditional ecological concepts and methods are seldom directly relevant to major problems with renewable resources and the natural environment. What is proposed as a partial framework for a more comprehensive, planned transdisciplinary approach is elaborated in some detail. Current issues with Canadian fisheries are used to relate the concepts to practical concerns.

Résumé

REGIER, H. A., P. L. BISHOP, AND D. J. RAPPORT. 1974. Planned transdisciplinary approaches: renewable resources and the natural environment, particularly fisheries. J. Fish. Res. Board Can. 31: 1683–1703.

Les écologistes, qui ont cherché pendant longtemps un plus grand rôle pour leur science et leurs vues dans le processus de prise de décision, voient enfin la voie ouverte. Mais on commence à réaliser que les méthodes et concepts écologiques traditionnels ont souvent peu de rapport direct avec les problèmes majeurs que posent les ressources renouvelables et l'environnement naturel. Les auteurs élaborent de façon quelque peu détaillée ce qu'ils proposent comme cadre partiel d'une méthode d'attaque transdisciplinaire planifiée, plus vaste. Ils font appel aux problèmes courants des pêches canadiennes pour établir une relation entre les concepts et la pratique.

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Introduction: The Broad Context

Planning, Research, and Science

In Canada and elsewhere the capability for large-scale and long-term planning is gradually developing. Trist (1970) recognized this process as an integral part of western society's evolution into postindustrialism. Galbraith (1973) noted that the personal security of senior officers of large corporations, of the civil service, and of other major social institutions could be enhanced by collaborative planning. Ecologists concerned about environmental disruption, shortfalls of renewable resources, and the well-being of future generations (in ways not typical of Malthus's writings) have published "survival plans." Some of the earlier "plans" of environmentalists can be characterized fairly as ideological manifestos, but more formal and rigorous planning procedures are gradually coming into use. "Concerned ecologists" may fear that their activities on balance might be subverted by more competent planners with other biases and objectives, e.g. the personal security of the managers of multinational corporations.

In Canada the usual response to calls for action on major problems only recently perceived has been to create a new institution or agency, or adapt an old one, for each major problem. The approach is used to isolate the problem, to contain it, and to deal with it in an ad hoc manner. The resulting welter of criss-crossing mandates and responsibilities greatly reduces the freedom to act effectively on any new problem. With respect to the natural environment and renewable resources in Canada, institutional gerrymandering is still more acceptable politically than is explicit rational discussion and planning.

Planning procedures are gradually being introduced at all the hierarchic levels within the Canadian democracy (MacKenzie 1974). Much of the planning heretofore has been of a geographic nature such as town, city, and regional planning. Much of the latter has been, directly or indirectly, a service to entrepreneurs such as private developers, with relatively little emphasis placed on creative long-term planning within broader social contexts.

Many scientists have participated in intensive studies of Canadian science and technology policies (Lakoff 1973; Hayes 1973). In the past much of our science has been curiosity-directed; some of it has found application as a result of "supply-push" mechanisms. Government-funded research is coming more and more to be related explicitly to practical problems in a mission-oriented or "demand-pull" mode.

For the foreseeable future a more complete mobilization–integration of research than heretofore seems inevitable. Though such a process has been much decried, the opportunities for doing first-rate science and for applying it efficiently and effectively may be greater than in recent days of ad hoc laissez-faire. It all depends on what the rules of the new game will be. Under the planning procedures now developing academic scientists and researchers not only have the opportunity but also part of the responsibility of determining the rules and for assuring that they are administered fairly. This duty calls for broad objectivity, fairness, and political courage — characteristics that may not be universal among scientists.

Hierarchies, Disciplines, and Conceptual Frameworks

A basic feature of the conventional paradigm of science, — whether the subject matter is physical, the earth, life, behavioral, or political, — is the axiom that hierarchic stratification and structuring permits the most effective division of labor. The way in which scientific disciplines have arisen, evolved, and sorted out their respective roles or niches is mute evidence of how this feature of the paradigm permeates all our science. Each discipline maintains an internal hierarchic conceptualization and perceives itself as one component, perhaps the most important component, within a larger hierarchy. But a formal or tacit division of labor within or between disciplines should always remain tentative, else it ceases to be a convenience and becomes a constraint.

We are now well into a process of resorting and restructuring intellectually and institutionally. This has been one of the implicit goals of the environmental renaissance of recent years, but is more extensive than that in motivation and scope, as already indicated. Some of the recent events include: a form of organization in some of the newer universities not fully congruent with the disciplinary taxonomy and structure of older universities, a proliferation of interdisciplinary institutes and courses within those universities in which the old-style thinking on disciplines remains as though cast in concrete, reorganizations in government that

have cut through old department–discipline alliances, new kinds of nongovernmental organizations.

This is not simply some minor housecleaning within the ivory tower. The status of various disciplines within the pecking order of the power hierarchy is changing, in academe and elsewhere — with hurt to some and temporary trauma to all. To some extent the process is a struggle between reforming forces and vested interests; to recognize this is to take the first step toward mitigating unnecessary trauma.

Environmentalists concerned about pollution, our health or that of other living things, as well as ecologists worried about the state of various resources, knew long ago that their campaigns implied a thoroughgoing intellectual as well as an institutional reformation (Fig. 1). Considering how far the process has already come, there should be an adequate basis of experience to permit some effective forecasting of how the reformation might continue.

Rational planning requires that self-consistent goals be stated which implies existence of a high-level conceptual framework. Somewhat paradoxically, rational planning as now generally practiced assumes that all frameworks will remain partial, incomplete, and then become obsolete. The minimal goal of planners may be to reduce the amount of confusion, frustration, and trauma inevitably associated with the political process. A tentative conceptual framework then becomes the playing court, with its structures, within which all prospective intellectual protagonists can participate fairly in the intellectual part of the political game. Sophisticated games can perhaps be played in very primitive courts with shoddy equipment, but under these circumstances a large random component or bias will occur in the game as it is then played.

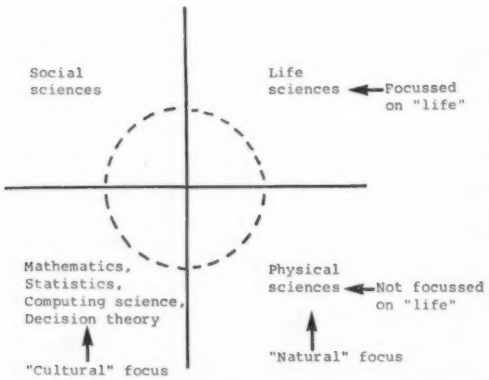

FIG. 1. Four scientific macrodisciplines nested according to two ancient dichotomies here sketched as orthogonal to each other. Current problems with renewable resources and the environment are difficult to resolve, in part because they straddle both dichotomies, as implied by the dotted circle. McHarg (1969, p. 197) casts a larger conceptual net: he refers to ecology as "the science of the relations of organism and the environment, integrative of the sciences, humanities and the arts — a context for studies on man and the environment."

FROM INTRADISCIPLINARY TO TRANSDISCIPLINARY RESEARCH

We may recognize three classes of science and scientists: intradisciplinary, inter- or multidisciplinary, transdisciplinary.

a) Intradisciplinary scientists work fully within one of the traditional disciplines such as biology, chemistry, geography, economics.

b) Inter- or multidisciplinary workers commonly anchor themselves firmly within a traditional discipline but venture out, perhaps under inducement of some appropriate recompense, to conquer conceptual area in some no-man's land between disciplines, to forage for new insights, or to form an alliance to achieve some common ends.

c) Transdisciplinary scientists may haul up stakes and march off secure in their broader understanding of the scientific method. They may address questions large in scope and of apparent high complexity unruffled by the defenders of the interests of various disciplines who may in the past have defended special claims to some parts of the problem area.

Table 1 illustrates a suggestion that a "maturity" variable, defined over the set of all scientists, may have an approximate relationship to the intra- to transdisciplinary variables sketched above. The table should be interpreted in this way: to be effective a scientist working at the ASA trans-

TABLE 1. An expository model relating disciplinary scope to the orientation of applied scientists at different "maturity states." Asterisks identify the main foci of activity.

Maturity states in applied science: orientation	Disciplinary scope		
	Intra	Inter or Multi	Trans
Information and data	*		
Technique and methodology	*	*	
Hypotheses and models		*	*
Specified goals		*	*
"Applied systems" analysis			*

disciplinary level must have expert insight into all other levels, while a worker to be effective in collecting and summarizing data need know very little about ASA. Thus the ASA–transdisciplinary worker must have the richer experience, hence be more "mature."

Some further elaboration may clarify what is implied in Table 1.

Information- and data-oriented — Disciplinary collaboration may be limited to the very preliminary steps of scientific endeavor. As with the "layer-cake approach" to regional planning (McHarg 1969), the collaboration may end when each narrow expert has summarized his data so that they may be entered into an agreed-upon format, whether table, matrix, map, or computer data bank. Alternatively, each worker could on intuitive bases recommend a series of variables to be monitored; the resulting time series data would hopefully be useful for decision making in the future. The analysis beyond such relatively unsophisticated stages may not be formally structured.

Technique- and methodology-oriented — An intradisciplinary expert may undertake a project of larger scope than can be addressed conveniently within his discipline. He may then co-opt experts from one or more other disciplines to help identify constraints within his own approach and to join in the attempt to relax those constraints.

A number of intradisciplinary experts from different disciplines may join in a game, the object of which is to get whatever insight one can from the others and also to gain the advantage that will permit one to specify the approach to be taken with respect to the problem of common interest. Constraints may be placed on the tactics that may be employed during the course of such an adversary game, as in the case of the Delphi conventions.

Economists seek to quantify alternative solutions to a specified problem from the viewpoint of an agreed value system whether at the individual, corporation, society, or some other level. They may attempt to quantify uncertainties using decision theory.

Hypothesis- and model-oriented — The working hypothesis implicit in "applied science" is that for any perceived problem a number of models (hypotheses, theories) can be created that take explicitly into account all the major variables and are so structured as to permit an analytical solution of the problem. Depending largely upon the personal preferences and previous training of the experts involved, the models may be cast as deterministic response surfaces, stochastic Markovian sequences, dynamic functional mechanisms, explicit decision processes, etc.

In the unlikely event that all variables can be reliably transformed to a common scale, e.g. dollars or beaver skin, one or more of the existing economic models may be fully appropriate for what was initially taken to be a complex interdisciplinary problem. More commonly with major problems, economic models and analyses will be nested within more comprehensive models of social institutions, geography, ecology, climate, etc. Considerations in those other areas are often taken to be constraints in economic analyses; these constraints can be developed into the basic skeleton of the more comprehensive model to which economic analyses may then relate in an explicit manner.

In recent years numerous scientists, who are themselves not constrained by the boundaries of a particular conventional discipline, have found that some models developed in different disciplines are broadly congruent or conceptually homologous. With further study this phenomenon will itself be modelled in a transdisciplinary context. Interdisciplinary mobilization on a particular problem can then be planned explicitly from a higher-level viewpoint.

Goal-oriented — Much so-called interdisciplinary work is being undertaken on crisis problems. The goal is to resolve the crisis, perhaps with the fall-back position of surviving the crisis. Questions of research efficiency, reliability of findings, or scientific elegance, may be assigned so little importance as not even to be mentioned. The logic and methodology may be uncritical and haphazard; understanding colleagues may look the other way while the participants are usually paid well for their collaboration. This primitive stage may soon be over (Banfield 1973).

With the gradual development and consolidation of the "planning system" in Canada — in large corporations, in civic organizations, in government, etc. — explicit transdisciplinary contexts are being created around major specified goals or targets. Demand–pull mechanisms for stimulating and supporting specified kinds of interdisciplinary science are being developed. The forms that effective institutions might take are being discussed (Cellarius and Platt 1972).

ASA-oriented — The "applied systems analysis" (ASA) approach is to be as objectively and comprehensively scientific as possible, i.e. to be unconstrained by the traditions and practices of various disciplines and schools. Relevant goals, models,

and methods are all considered in a systematic, often iterative, process with the aim of finding an objective, efficient, and reliable way of solving the problem. The process of defining and solving the problem is a "system" with loops of various kinds. The approach may be broadly eclectic or radically innovative or both with respect to models and details of the experimental method.

More about "Applied Systems Analysis"

Raiffa (1973) has described ASA as follows:

"ASA...involves the use of techniques, concepts and a scientific, systematic approach to the solution of complex problems. It is a framework of thought designed to help decision makers choose a desirable (or in some cases a "best") course of action. The approach may entail such steps as:

a) recognizing the existence of a problem or a constellation of interconnected problems worthy of and amenable to analysis;

b) defining and bounding the extent of the problem area. It is necessary on the one hand to simplify the problems to the point of analytic tractability and on the other to preserve all vital aspects affected by various possible solutions. The difficult judgement upon the inclusion or exclusion of problem elements — balancing their relevance to the analytical grasp of the situation against their contributions to manageable complication — often determines the success of systems research;

c) identifying a hierarchy of goals and objectives and examining value tradeoffs;

d) creatively generating appropriate alternatives for examination;

e) modelling the...interrelationships among various facets of the problem;

f) evaluating the potential courses of action and investigating the sensitivity of the results to the assumptions made and to facets of the problem excluded from the formal analysis;

g) implementing the results of the analysis.

Precisely because ASA is a rational approach rather than a technique, the list of steps above should be understood in a qualified sense. Not all the steps need be included in every instance of responsible system analysis. Some steps may be handled in a more formal manner than others," etc.

So far, Raiffa. Actual experience in performing applied systems analysis according to this model (in essence) has been summarized and analyzed by Holling and Chambers (1973). Within Canada's Fisheries and Marine Service, two projects of this type are currently in the planning stage — the Strait of Georgia Project and the Gulf of St. Lawrence Project. Canada's plans within the Man and the Biosphere Program (MAB), are essentially of an ASA nature.

The details of identification and solving of actual problems, within the natural resources field, using ASA is not the primary concern of this paper. To what extent ASA should be stimulated and supported, and how various stimuli might be applied and modulated, are relevant to the strategic or policy levels of decision making. Appropriate guidelines on these questions will emerge iteratively as a result of experience and evaluation within successive cycles of the larger planning process.

This paper focuses on the kind of science that we expect will be directly relevant to the larger problems concerning the natural environment and renewable resources. Decision-making strategies have not been treated explicitly; the recommendations of Bella and Overton (1972) seem particularly appropriate on matters where catastrophes and major mishaps are otherwise foreseeable. How the kind of applied science here discussed may be organized effectively has been treated by Weir and Munroe (1966), Holling and Chambers (1973), Mar and Newell (1973), and Mar (1974). Concerning fisheries, we believe that our proposals are generally consistent with those of Kesteven (1972), Rothschild (1974), and MacKenzie (1974).

Toward Transdisciplinary Frameworks

Additional features that useful conceptual frameworks must possess may be inferred from less-than-satisfactory efforts at accommodating new forces such as "ecology" heretofore. The seven sections under this heading provide both a diagnosis of what is inadequate about previous efforts and a prognosis of some characteristics that the new approaches will likely exhibit.

Problem Complexity

As the ecological reformation has begun to take hold, a complaint reiterated ad nauseum pleads that the problems being identified are all so terribly complex. What is really being deplored is that the old approach to these problems — simply to ignore them, or to place an ad hoc institutional box around and over each in the hopes that each can be resolved in isolation, or to override them by relying on the brute momentum of dominant institutions — no longer works; also that yesterday's acclaimed expert does not know how to deal with them as bona fide issues (Chant and Regier 1972). Such pseudocomplexity, stemming primarily from raw ignorance and the inadequacies of the conventional wisdom, is not the concern of this section.

As indicated by Raiffa (see above) all problems are not equally difficult. Some screening mechanism may be conceived that would help to sort problems objectively into different classes of difficulty, or a number of screens that are conceptually orthogonal

or independent might be used to sort problems into a two- or three-dimensional ordering, if this is seen to be useful within the broader process. The development of such a mechanism and servicing to ensure its proper functioning, might well be a strategic responsibility.

Cartwright (1973) has produced a context that neatly interrelates problem complexity, research challenges, and likely limits of action in the short-term (Table 2). Raiffa's full description of ASA appears to relate to what is termed by Michel Chevalier a "metaproblem" (Cartwright 1973). But Raiffa does imply that less difficult problems may not require the full gamut of formal ASA steps. Clearly the choice of major methodological components of the operation to be mounted in studying a particular problem is an important decision, and Cartwright's formulation may be useful in approaching it objectively.

The commonly stated guideline, that a solution to a problem must be of the same order of complexity as the problem itself, may need some further clarification. With an inappropriate or inefficient context, a problem may be viewed as almost hopelessly complex; the solution may then be formulated as a jumbled mix of ad hoc responses to the more visible aspects of the problem. This kind of "solution" may be so "complex" as to have essentially no rationality whatever. The principle stated above should obviously have a prior condition that the problem be addressed in a context relevant to the problem, not just any context, whether conventional or radically new. Given that a first step of choosing the appropriate context has been accomplished with intelligence the degree of complexity of the problem as then perceived and the degree of complexity of the measures or protocols necessary for its effective solution can be expected to be comparable.

Scope and Scale

Within any ordered, cyclical research and decision-making process, whether within ASA and solving problems in the field or within the context of planning where major institutional matters are resolved, the questions of scale and scope rapidly materialize. But they are seldom addressed explicitly, at least within fisheries work. By scope I refer to the overall dimensions conceptually (and/or spatially and/or temporally) of the models employed in the research; scale refers to the relative magnitude of the units of measurement employed with particular variables included in the model, i.e. the inverse of the "degree of resolution" or precision. Paulik (1972) and Holling and Chambers (1973) have discussed aspects of this question.

Elaborating the point further, research models of particular components of a process may be of much greater scope and of grosser scale than is appropriate to the nature of the problem. Conversely, relatively delicate models or intricate assemblages of delicate models may be devised where something more robust is in fact required. Where models and problems are mismatched, research will eventually provide some useful information but at relatively high cost.

Table 2. Limits of analysis and action by type of problem (modified from Cartwright 1973).

Has an adequate model been developed?	Are all variables readily measurable?	Type of problem	Limits of analysis	Limits of action
Yes	Yes	1. Simple	Comprehensive and adequate in practice	Maximization or optimization
No	Yes	2. Compound	In-depth analysis of parts of problem	Suboptimization "second best"
Yes	No	3. Complex	Broad, imprecise understanding	Overall improvements
No	No	4. Meta-problems	Identification of points of departure, set benchmarks	Partial improvements

In fisheries work serious mismatches of model and problem are now the rule rather than the exception, although the mismatching is beginning to be recognized as such. In particular certain macroproblems now facing Canada's fisheries scientists are by and large being addressed in terms of scientific micromodels. (By "macro" I mean of large dimension conceptually; c.f "meta" as used by Chevalier which refers to a large measure of bona fide complexity.) The following series of 10 macroproblems may serve as a checklist to test the above contention.

1. Cooperatively with other disciplines, ecologists must devise effective management and regulatory guidelines for fishery exploitation to maximize resource rent or some other social index or indices. Most basically, the common property problem must be solved conceptually and in practice. This involves both "open access" and "multipurpose" aspects. The scale and scope of the ecological models must be consistent with those of the economists, sociologists, political scientists (re law, regulations, institutions), etc.

2. More particularly, if Canadian sovereignty is extended to the edge of the continental slope then we will be expected to manage a mix of interacting species resources being harvested by a mix of interacting fisheries interests. In the foreseeable future it will be possible to model fully only a minority of the fish species involved using population dynamics concepts and then only where the various species interactions are "simple" as judged by the population dynamics paradigm.

3. The "new frontier" of the oceans may yet involve us in the classic frontier-type scramble for resources using the only technology available, which will be highly inefficient and will "quite accidentally" severely disrupt the life support systems of some of the fishery resources. Macromodels are needed to predict the likely impacts of this new manifestation of a process now several hundred years old in North America.

4. Another new frontier, the North, poses similar demands for macromodels, for "environmental impact assessments" for proposed major industrial developments. The difficulties being experienced to date in producing useful assessments relate in part to the fact that the ecologists involved attempted to apply micromodels that were quite inadequate.

5. Fisheries ecologists have called for pollution abatement programs but have great difficulties predicting how the aquatic ecosystem, or the fish community component of it, will respond as pollution loading rates are reduced, or loading regimes are altered. Community indices or variables should be modelled as a function of loading rates by various nutrients, toxic materials, acids, etc.

6. Aquacultural initiatives are being encouraged, particularly in the inshore areas of the seas and estuaries, and in freshwater bodies. These habitats are highly vulnerable to stresses from conventional onshore practices, e.g. urban, industrial, or agricultural wastes; stream flow modification; port construction; etc. Also the inshore habitats, whether in salt, brackish, or fresh waters, are of critical importance to a number of valued fish species. Clearly multidisciplinary macromodels are needed for inshore habitats.

7. Recreational uses and tourist industries will be expanded or intensified in remote areas, into the marine habitat, etc. If these enterprises are to benefit native peoples, existing fishermen, and other present users, as well as others in society, then a more effective and more comprehensive understanding is essential.

8. Urban complexes are growing and with them the inevitable, uncontrollable problems of urban runoff and atmospheric modifications, as well as demands for nearby recreational facilities and areas. Fisheries ecologists will need to address themselves to the question where such urban complexes should be sited — a macroproblem.

9. Agriculture is becoming progressively more intensive and will continue to do so for at least the next five decades. Already pesticides, fertilizer runoff, drainage from feed-lots, etc., are creating major problems for fisheries. Agriculturalists should be assisted to develop procedures to minimize impacts on aquatic systems; what is needed is an appropriate environmental impact model for each major agricultural option.

10. Last, but not implying a low priority, the desirability of preserving a series of native ecosystems in wild state in perpetuity requires a set of criteria, or a macromodel, of the ecological values associated with such a program.

The question of appropriate scope can itself become complex. Emery (1973) has remarked that major practical problems to be researched and resolved may themselves arise from a serious mismatching of the scopes of two social processes both important to the decision-maker. This may frequently be the case within fisheries. For example eutrophication may trigger a phase-change or transformation of an entire multispecies fish community while the harvesting, trade, and regulatory process remains geared to individual species populations or to closely related species groups. Pulse fishing and its consequences may be another case. The effective approach may be to organize the problem at the outset so as to fully encompass

the largest unit of interest. This was in essence the perception and stimulus for our Symposium on Salmonid Communities in Oligotrophic Lakes of 1971 (Loftus and Regier 1972).

Some of the considerations in this section may be summarized and perhaps clarified from a somewhat different perspective. Table 2 may be related in the first instance to items numbered 1 and 5 in this section, but similar considerations apply to the others as well. As with Raiffa's ASA, the contents of Table 3 as formulated are useful basically for expository purposes; any slavish adherence to it would be unfortunate.

Multidisciplinary Interaction

Many of the problems now facing society, and fisheries workers, are of a scope and complexity such that they simply extend far beyond the bounds of any single scientific discipline (e.g. fisheries biology, economics, ecology, political science, law, etc.). Within Kuhn's (1962) paradigm, it may be inevitable that any or all of these disciplines will and should in time cease a separate existence in order to amalgamate, to be extinguished, or perhaps to evolve into something qualitatively quite different. Though that is the long-term prospect, the short-term reality is quite different, perhaps because of the massive inertia of the older universities in this respect.

The realistic option is held to be a rather coy liaison between two or more disciplines on problems of major social significance. Such a liaison can take one of a number of forms, not all equally useful from the viewpoint of the matchmaker.

In the present context the objective of multidisciplinary collaboration is to solve important problems — hence problem-solving capability is what is desired. Such a capability (PSC) may be perceived as being a function of: technical competence (TC) deriving from education, training, or past experience; existence of appropriate theory (AT) or relevant models and methods derived in the most part by others in the discipline(s) of interest; and accessible data (AD) already in store or readily measurable in situ. Symbolically:

$$PSC = f(TC, AT, AD)$$

Much of our science is compartmentalized into "disciplines." Within a discipline there is generally some redundancy in that a number of "traditions" and/or "schools" are implicitly encouraged (or at least tolerated) to develop and compete. Within a particular "school" and with respect to particular practical problems of special interest to a "school," TC, AT, and AD tend to evolve as a coordinated and mutually congruent set with respect to scope, scale, special techniques, model characteristics, etc.

Let us identify a particular discipline by the subscript i, and a tradition within a discipline as j. (Ignore the third tier in the hierarchy, i.e. "school" — it only complicates the subscription.) One strategy for generalized problem-solving would

Table 3. Some general interrelationships between problem scope and other relevant planning variables.[a]

Problem scope	Small	Medium	Large
Time perspective	Short	Medium	Long
Geographic unit	Point source	Ecosystem	Sub-national region
Ecological unit of analysis	Organism, population	Guilds, community	Ecosystem, biome
Major technical activity	Monitoring, assessing, control	Analyses, transferring and applying science	Interdisciplinary study, forecasting and planning
Absolute precision	High	Medium	Low

[a]This approach was developed by a committee of the Institute of Ecology; J. F. Rimberg and J. M. Neuhold in particular contributed to its development.

be to identify and select the most effective and efficient among the PSC_{ij}. Symbolically:

$$\underset{i,j}{\text{select optimum}} \left(PSC_{ij} = f(TC,\ AT,\ AD)_{ij} \right)$$

This results in selection of the best discipline-tradition combination for a particular job; it ends as a unidisciplinary approach following interdisciplinary competition.

Implicitly, the above approach has been used until recently in fisheries, and "fisheries biologists" of the locally dominant tradition have addressed any particular problem essentially alone. In water resource development in the USA during the early 1960's, cost-benefit analysis was the dominant tradition.

The multidisciplinary approach now being nurtured appears to rely on the existence of a number of traditions within each of a number of disciplines all of which are in some degree relevant to the practical problem. One or more traditions within each discipline, it is assumed, are conceptually congruent and of similar scope and scale to one or more traditions in some other disciplines, and to the problem of interest. The conceptually simplest case for the decision-maker would occur when each discipline would contain only one tradition that was congruent with only one tradition in each of the other disciplines, and with the problem being addressed. Clearly, if a multidisciplinary approach would then be undertaken, there would be only one candidate interdisciplinary approach available for selection comprising the union of the various single candidates from each discipline.

But suppose there are a number of mutually congruent sets, each with a different contribution from each relevant discipline. Identify such interdisciplinary congruent sets by the subscript k. Then the strategy is to select

$$\underset{k}{\text{optimum}} \left(PSC_k = f(TC,\ AT,\ AD)_k \right)$$

The situation may in practice be more complex. With appropriate interdisciplinary or transdisciplinary education and training, technical competence may be interchangeable between disciplines and, of course, traditions. Also, available theories in different disciplines may be seen as being isomorphic, or variants of the same theory. Even the accessible data may be mathematically transformed to be relevant within more than one discipline. This implies that a particular $f(TC,AT,AD)$ as conventionally identified already contains parts that are readily interchangeable with other sets, with respect both to disciplines, i and traditions, j. Under these circumstances, the organizer

$$\underset{l,m,n}{\text{selects optimum}} \left(PSC_{lmn} = f(TC_l, AT_m, AD_n) \right)$$

Here the (l,m,n) set ultimately selected may or may not include a component from each discipline. Because of the general desirability of a measure of functional redundancy, it would seem a good practice to duplicate each of TC, AT, and AD, yielding two PSC_{lmn}'s within a study of any major significance.

Again, the concerns of senior administrators on this point need not extend beyond ensuring that in fact problems are being approached in an objective, explicit, and defensible fashion. The details of the selection of appropriate problem-solving capability for major field problems would presumably be the responsibility of lower echelons. But the analysis above contains an implicit conceptualization of how a transdisciplinary approach may in time lead to new conventions in what might amount to a new macrodiscipline. It might be desirable to foster such an innovation (see below).

Isomorphisms and an Environmental Macro-Discipline

Rapport and Turner (1974) have for some years addressed the question of whether and to what degree theories and models already in use by some economists are in some sense analogous or homologous to those used by some ecologists.

Natural communities of organisms and human societies fundamentally face similar problems with regard to resource use. Resources are limited in both communities and resources possess many alternative uses. Therefore allocation mechanisms are required to distribute resources to particular uses. In both communities there are rewards to the efficient user of resources, profits to the entrepreneurs who produce at low cost, higher reproductive rates to the species which can obtain resources with the least expenditure of energy. The payoffs to organisms can be represented by fitness sets; to economic man, by "indifference curve" maps.

One of the many problems confronting those planning for the rational preservation of our planet is the lack of communication between those whose concerns lie with economic (growth) well-being and those who strive for our ecological well-being. A transdisciplinary framework for resource allocation

could permit insight into both economic and ecological community functions. A common language might be developed so that theoretical structures which exist in one area would be readily transferred to the other. Such a framework would simplify knowledge by condensing theories currently stated in terms of specific languages to a theory that can be stated in a single language thus joining two disciplines which have so far evolved on separate paths. This would then permit considerably more effective feedback among theory, monitoring, and policy.

Similarly, attempts have been made to bridge ecology and sociology (Emery and Trist 1973), ecology, thermodynamics and economics (see Georgescu-Roegen 1971), and others.

Progress in efforts to identify conceptual isomorphisms and to condense scientific theory and methodology should be of some strategic interest to government. Communication can be simplified and made much more efficient, multidisciplinary problem-solving teams need not be as large as would otherwise be the case; in general costs would be reduced.

In a Toronto speech in March, 1973, I. L. McHarg identified a mutually compatible set of disciplines and traditions related to environmental concerns and problems. These are: ecology, ethology, ethnology, certain traditions within human geography, aspects of cultural anthropology, and epidemiology. Certain traditions within economics might also be compatible to this set, e.g. works by K. E. Boulding and J. K. Galbraith. Individually and as a set the disciplines identified above tend to treat man and environment as mutually interdependent, but from a higher-level viewpoint. None is bounded by an artificial man–environment interface (see Fig. 1).

Efforts to create a macrodiscipline to encompass all of these units, now widely scattered within institutions such as the universities, the professions and government, might now be timely. To practical people such as engineers, lawyers, cost-benefit analysts, systems analysts, planners, and administrators there need be no threat in this suggestion. Quite the reverse! The intention is to provide broader, more encompassing, and hence more useful models in order that they may fulfil their responsibilities more effectively at less cost to themselves and their employers.

In part, a macrodiscipline might rescue us from the artificial man–environment dichotomy inherent in our culture with its counter-productive implications concerning our responsibilities with renewable natural resources and the ecological environment.

B. W. Mar (1974, personal communication) has stated that new disciplines may tend to be more concerned to protect their own boundaries and discipline uniquenesses than are the older disciplines. Such a process would reduce the mobilization suggested above with a negative feedback for future mobility. An alternative long-run tactic would be to stimulate tolerance among disciplinarians and provide greater incentive to write for broader audiences. In this manner the need for more journals would be contained, argues Mar, and the usual posturing between disciplines could be minimized.

Clearly the tendency for institutionalization to breed intolerance should be combatted wherever it occurs — within yesterday's dominant disciplines as within the newly dominant ones of tomorrow.

Statistical Sophistication

Several of the preceding sections have dealt primarily with the question of available theory; this section addresses aspects of technical competence and some facets of experimental design and sampling theory as related in essence to the intensity of the man–environment interaction. The section is based on work by an Ontario Regional Working Group of the 1972–73 Man and Resources Program (Regier et al. 1973).

By and large ecology has developed through time approximately as shown in Fig. 2. Perhaps because the overall trend was largely uncharted and unplanned, the process has been quite uneven among different traditions of ecology, broadly defined, such as meteorology, fisheries, forestry, soils, hydrology, etc.

The symbols used in Fig. 2 are defined as follows:

A_1: An inventory survey, undertaken by workers in a particular narrow discipline. A few factors and quantities of immediate practical interest are measured on selected sites over a broad area. Development of specific resources may be initiated on the basis of such data.

A_2: Assessments of the potential of natural resources, whether renewable or nonrenewable, or of skilled manpower, etc. This step is used in early stages of planning developments that require large social and/or capital investment; and in regulating resource use.

B: Assessments of the likely environmental impact of proposed large-scale developments. "Impact statements" are used in simplified socio-economic planning, e.g. in applying cost-benefit procedures.

C_1: Routine monitoring of indices, the mathematical definitions of which are derived from experience and scientific theories, of factors that

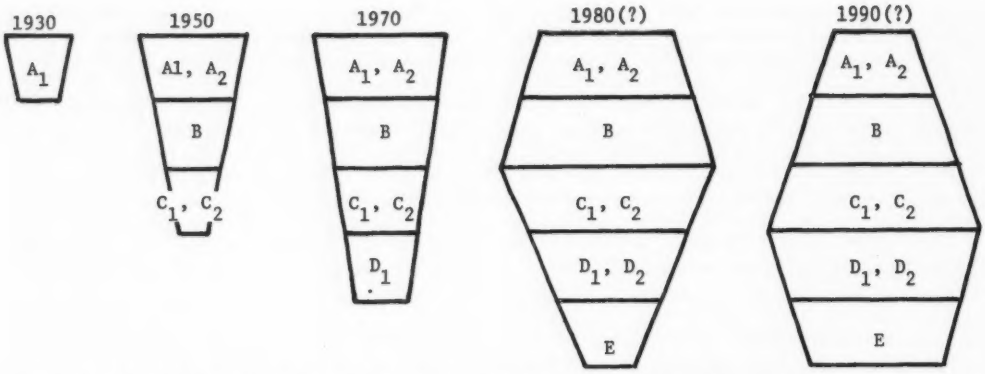

FIG. 2. The size of the various strata is a very approximate estimate of the effort (corresponding roughly to the cost to Canada) expended in collecting, processing, and applying corresponding data classes.

relate closely to the well-being of society from cultural, political, economic, or environmental viewpoints. Indices that measure fairly comprehensive factors over a broad area may be useful for longer-term projective/extrapolatory planning by government agencies.

C_2: Process monitoring and real-time control of some particular, important man–resource interactions such as the off-loading of noxious wastes or the harvesting of certain sensitive renewable resources. This approach tends to forestall overly intense stresses being applied within intensely interactive situations.

D_1: Step-wise, experimental management in which an explicitly formulated decision process uses information from past management experience and experiments, together with measurements of indices routinely monitored, to guide future management.

D_2: Formal functional analyses of components of man–resource problems as dynamic systems. Usually a number of disciplines collaborate. This phase is still largely experimental.

E: Integrated planning and decision making using formal analyses of policy alternatives performed as much as possible in a transdisciplinary context. A few trials have been begun in Canada in man–resource problems.

The trends sketched in Fig. 2 have the following five implications:

- From the early stages of economic development, where questions of resource potential and unpleasant aspects of the natural environment predominate, the data requirements have gradually shifted to what is needed to understand, order, and manage man's demands and impacts on specific resources and the environment.
- Single factor, simple resource, and separate discipline conceptualizations are supplanted by more comprehensive initiatives that also address complex interactions, using functional analyses of dynamic man–resource systems.
- Elementary scientific and technical methods appropriate at early stages are superseded by highly sophisticated and complex precisely ordered procedures, together with higher levels of concept coordination.
- Simple records stored in survey notebooks are eventually succeeded by data systems in a national network of electronic computers.
- The more highly a region is developed in a conventional "economic" sense, the more intense the man–resource and the man–environment interactions are likely to be, and the further along in the direction of sophisticated transdisciplinary procedures will the technical process need to be developed.

Figure 2 may be used as an approximate standard by which to judge the present state of the information–analysis–planning complex for certain major components of our man–environment and fisheries problems.

- Level A methods should be extended to cover all of Canada with respect to some factors and resources.
- Level B, refined into a step-wise procedure matched to other aspects of development planning, should be applied to all new developments.
- Level C methods should be expanded to greater parts of the more developed areas, and more types of information should be obtained in this manner.

— Level D approaches should be used more widely and facilities for the necessary technical training expanded.
— Level E research should be encouraged with a number of appropriately sophisticated groups across the country. The techniques should be developed to use "citizen input" as well as traditional "scientific" data.

Transdisciplinary Foci

Regier (1974b) has explored the question of how different types of major fisheries problems may be addressed by selecting appropriate "traditions" that already exist in the broad area of natural resource ecology and management.

A two-dimensional classification is presented in Fig. 3. The criteria of stratification are mean and variance, where the latter refers to temporal oscillations or fluctuations. For each of the four classes in Fig. 3 there already exists a number of alternative scientific and practical models and methods within the natural resource family of traditions. Some have not yet been adapted to fisheries situations, but this could be done expeditiously given an appropriate stimulus.

HIGH
Class D: Many small resources interacting within systems that are fluctuating due to pronounced non-constant natural and/or cultural stresses. Variability may be modelled as an "independent" variable within a set of similar systems. A major objective of management is to prevent the exploitation regime from developing a positive feedback interaction with other stresses, using a step-wise experimental approach. Examples: intensely exploited, polluted, fluctuating systems such as Great Lakes, Baltic Sea, some estuaries and bays.
Class B: A few large resources dominate; they fluctuate markedly — and constantly interact — as a result of large-scale noncyclic stimuli related to climate, oceanographic processes, the fishery, etc. Monitoring, Markov-like modelling, and probabilistic forecasting may be used to plan industrial activities so as to develop negative feedback mechanisms to control variability. Examples: clupeids, flood plain fisheries.
SMALL ← SIZE OF INDIVIDUAL SPECIES RESOURCES OR STOCKS → LARGE
TEMPORAL AND/OR SPATIAL FLUCTUATION IN BIOMASS COMPONENTS
Class C: Numerous small resources usually interacting ecologically in systems that are likely to remain relatively unstressed or that possess capabilities to accommodate expected stresses. Yield in toto or by taxon groups may be modelled as a function of large-scale natural and cultural variables; management may be explicitly experimental and step-wise. Examples: mixed resources in lakes, large reservoirs, near shore in seas, on reefs.
Class A: Several large stocks that are relatively independent ecologically dominate the ecosystem in which biomass components are quite constant and/or relatively unresponsive to moderate stimuli. Resource use may be optimized separately stock by stock using population dynamics techniques. Examples: marine benthic taxa, tuna, whales, anadromous salmonines.
LOW

FIG. 3. A conceptual model of four major clusters of problems related to fisheries exploitation. An analogous model may be used to classify pollution problems where pollutant loading takes the place of stock size or biomass.

It seems clear that the "population dynamics" tradition, conventionally the dominant and sometimes sole tradition applied to a particular fisheries problem, is really only effective and efficient with Class A situations. This class may now include considerably less than half the situations in which major problems are emerging within world fisheries. If so, it should be of strategic concern that effective scientific models and methods be adapted and refined for classes B, C, and D, without sacrificing the necessary emphasis on Class A approaches where these remain appropriate. Perhaps the first priority would be systematically to search out appropriate approaches in related disciplines and adapt them to fisheries situations. The stimulus from such an exercise might fortuitously result in the creation of novel approaches — if so, so much the better. But much can be accomplished without any further basic innovations. In other words, the work of identifying and developing further a number of alternative approaches for each of the four classes in Fig. 3 can now be planned, costed, and programmed with some degree of objectivity.

A preliminary examination of social, political, and economic (industry and trade) features associated with problem classes A–D suggested that various traditions within these disciplines could also be usefully stratified in this manner. If so, then this would be an instance of large-scale isomorphisms, across disciplines, and would provide useful cues on how multidisciplinary teams might be structured for major problem classes. Thus, risking oversimplification, four classes of multidisciplinary teams might effectively cover all the major problem types with "conventional" exploitation and management. Not just any multidisciplinary assortment, even within the constraints specified in the section on "Multi-Disciplinary Interaction" above, will do. But four (and only four) different classes of problem-solving capability may be sufficient. Thus some transdisciplinary specialization might already be possible and also desirable.

A further isomorphism may be of interest. At present, and from the vantage point of the population dynamics tradition, problem classes A–D correspond in sequence to Cartwright's problem types 1–4 described in Table 1 above. But given appropriate models, each of classes A–D can in theory be reduced to a type 1 problem. At least that is the hope of applied scientists.

We hasten to add that no problem is ever settled permanently from the viewpoint of Kuhn (1962), as elaborated by Grabow and Heskin (1973), Emery and Trist (1973) and others. Rather, it can be solved for the time being, within the context of the present temporal Gestalt and institutional arrangement.

The ecological level-of-organization at which a problem should be addressed may be taken up again here. Three tiers have come to be accepted in ecology as in some sense "natural" hierarchic modes: whole organism, species population or stock, ecosystem. Some ecologists identify an additional level — a guild of taxa that are fairly closely related within the evolutionary paradigm, and/or are closely related ecologically (see Loftus and Regier 1972). But this intermediate level between population and ecosystem may be ignored for purposes of this paper.

The matter of ecological level-of-organization may be seen as a further elaboration of the discussion of scope and scale.

Regier (1974a) has reviewed the present status with respect to fisheries interests of the science of whole-organism ecology (autecology, physiological ecology, physical factors ecology, etc.), population ecology (population dynamics, population genetics, "natural history," etc.), and ecosystem ecology (succession theory, stress responses, stability, etc.). An explicit stratification might well permit more useful planning; it may be desirable to induce universities to balance their undergraduate and graduate programs in this respect. Because universities now tend to work within this hierarchic context, rather than that depicted in Fig. 3 or treated in any of the preceding discussion, and because of their inertia will continue to do so for some time, selection of recruits for mission-oriented research may be improved by noting the manner in which competence in the ecology of a particular level of ecological organization relates to a class of practical problems.

Models and Hypotheses

The term model has come to be used very broadly. A number of classes of model may be identified all of which may be related to the theme of this paper.

Expository models are concepts developed to an operational stage particularly useful for problem identification and definition. Statistical models may be used in the analyses of time series or sets of survey data to produce a ranking of importance of a series of variables identified as relevant to the problem's solution. Functional dynamic models incorporate "causal mechanisms" (hypotheses of which often emerge from statistical analyses) to simulate and explicate more fully the processes contributing to the problem. Fourthly, in situations that are poorly understood, a model that permits exchange of parts may be developed to accept a range in the

selection of variables, modules, process constraints, etc. The latter class of model may permit a large-scale sensitivity analysis to indicate where research efforts are most needed.

All four classes of models are applicable, under the appropriate circumstances, in the applied systems analysis (ASA) approach discussed earlier. Which class or classes are most directly appropriate may be inferred using the conceptual analytical approaches elaborated earlier in this paper.

Following a selection, or trial choice, or a particular model class, the next decision concerns which of a number of alternative models already available should be selected, or whether a new model should be created on the spot. Any model chosen to aid in the solution of a practical problem becomes explicitly an hypothesis with respect to that problem and its applicability should be tested prior to its commitment to that problem.

The method of searching out, or generating de novo, some potentially useful models has itself been analyzed (Regier 1974c) and will not be treated further here.

Institutional Aspects

Some far-reaching institutional changes have occurred recently in Canada and elsewhere related to matters discussed in this paper. A sketch of these is presented, followed by a more conceptual analysis of what might be expected to follow from these changes.

Canadian Perspectives

The nature of the Canadian institutions dealing with major environmental and natural resource questions, and their relative importance within the political system have changed in recent years. These changes may be analyzed as part of a mobilization concerning questions now recognized as of major practical significance. Limited partial mobilization had occurred earlier during the past century on matters related to agriculture, forestry, fisheries, wildlife, sewage-borne epidemics, etc. The present mobilization is of a much greater scope, but not only because of the significance of the ecological problems per se: the emergence of environmental and renewable resource issues happened to coincide more or less closely with an explicit move towards formal planning in government.

Even a decade ago the institutional mechanisms for supporting ecological science and stimulating its application to practical problems were quite simple. By and large ecological scientists worked individually or with small numbers of students and/or technical assistants on small-scale theoretical or practical questions. Each communicated more or less directly with decision-makers whose role in turn was quite limited. With respect to renewable natural resources, such as fish, the role of the ecologist plus decision-maker concerned such matters as increasing, by minor adjustments of regulations, the general efficiency of a highly dispersed primary fishing industry harvesting a common property resource. The industry itself was largely at the mercy of the market system within the national, or international, economy. Thus the ecologist's task was to render a service to an unorganized and essentially weak component within the market system — itself a weak segment of the national economy (Galbraith 1973). A somewhat analogous situation applied with respect to "pollution."

Many problems involving ecological aspects are simply too large and comprehensive conceptually to be addressed effectively by a single scientist, no matter how expert. Hence increased organization was a foregone conclusion, as was an upgrading of the political status of the relevant governmental agencies.

Considering that the above development was superimposed on the gradual emergence of explicit planning in government, it may be seen that the role of the ecologist, say the fisheries ecologist, has within a decade shifted from a) that of servicing elements of an industry largely subservient to the market system to b) that of collaborating within a major component of emerging regional planning systems. Planners are already attempting to restructure social and economic institutions that will relax the market system's bonds on the primary industry.

Relating the above institutional transformation to applied system analysis, it seems clear that the methodology by which teams of workers will increasingly be organized on major ecological issues will approximate that of ASA. The planning system now developing may simply dictate that this will be the case.

Canadian ecologists have had relatively little experience with full-fledged ASA, at least within Canada. Simplified versions have been used: a "layer-cake approach" to regional planning, compartment-flow models to simulate macroaspects of a geographical region or microaspects of a lake ecosystem, long-term monitoring and modelling of river flows or fish harvests, simple assessments of major environmental impacts, etc.

In comparison to Canada, USA efforts, both those conceptually partial and those more complete, have progressed considerably further. Much of the technical competence on ASA that now exists in Canada amongst ecologists has been imported from the USA either by returning Canadian students or by American immigrants. Progress in other parts

of the world appears also to lag behind U.S. initiators.

Following up a strong interest in international environmental matters at Stockholm and in other fora, Canadians became active in the planning of UNESCO's Man and the Biosphere Program (MAB). This program is in essence an ASA approach focussed in ecology. Canada's international activities were not balanced by a fully effective start on a MAB program within Canada. Some members of Canada's MAB committees had only a very partial understanding of what was involved in MAB's ASA-like approach. Other members appeared to be frightened at the comprehensiveness of some of the proposed programs. Many had no real sense of the role that was developing willy-nilly within Canada and elsewhere for organized teams using an ASA approach. Under these circumstances, it may not seem strange that Canada MAB had difficulty presenting a compelling case to the government for adequate funding.

But the Canadian ecologists' limited perspectives and initiatives with respect to MAB may not be the whole story. The political debate and interagency struggle as to who if anyone should be responsible for funding such research may also have slowed progress in this matter.

Lest it be inferred that progress in effective ecological ASA would be rapid and almost automatic in Canada with adequate funding, e.g. given the MAB plans and competence originally imported from the USA, it may be stressed that the methodology of ASA itself now needs careful assessment. The one or two Canadian ASA efforts and numerous American attempts during the past 5 years have been accompanied by considerable trauma, some outright failures, and only limited success at best. Assessments of attempts at partial ASA's and of the more complete ASA ventures, are now appearing in the literature. These need to be studied carefully and any plans for future ASA's must include measures to forestall the predictable difficulties (Mar and Newell 1973; Holling and Chambers 1973).

As the "planning system" develops within Canadian governments it appears likely that ASA's will be initiated and carried out with increasing frequency. The technical competence to perform ASA's will need to be developed further as ecologists and other disciplines will progressively be mobilized into ASA teams.

Interactions between Universities and Governmental Agencies

The expository model and dynamic depicted in Fig. 4 and 5, for interactions between such institutions as universities plus research organizations

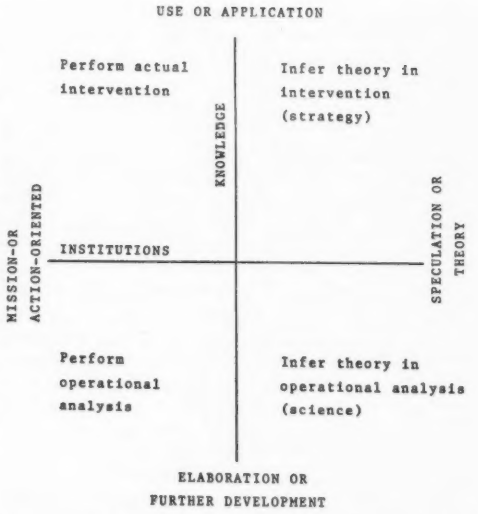

FIG. 4. The quadrants identify four major types of complementary activities that may result from effective use of knowledge by institutions.

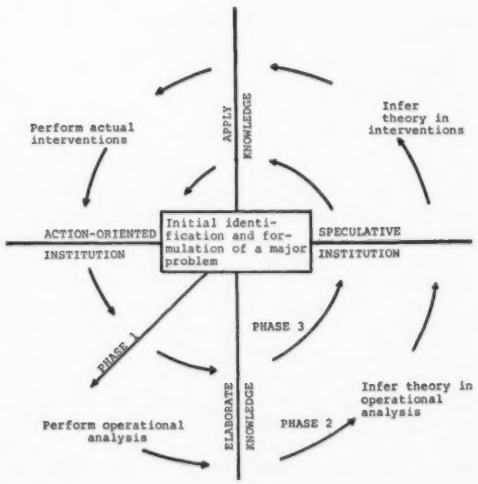

FIG. 5. The phase sequence of institution–knowledge interactions that will likely occur, implicitly or explicitly, in the course of solving a major problem. The overall paradigm will be man–environment interrelatedness. Phase 1 may be termed formalization; the phase 2 circuit is research iteration through experimental intervention; phase 3 leads to policy articulation and routine program delivery.

and action-oriented agencies, has been discussed at York University by environmental study groups.

In Fig. 4 and 5 the two dimensions of the paradigm are knowledge and institution. The institution dimension moves from mission- or action-orientation to speculation or theory. Similarly, knowledge is defined on a gradient from use or application to elaboration or further development. Through such knowledge–institution definition, one is able to focus on major phases in the management of large scale problems in man–environment interfaces. Analysis, always based on a theoretical construct, is then given a control or positive feedback correlate by means of theory in analysis. In turn, theory in analysis is controlled by theory in intervention (strategy), and theory in intervention by intervention. The processes can be further iterated by emphasizing actual intervention as it relates to operational analysis, achieving a "spiral" effect in a third dimension, which culminates in problem solution, strategy, or policy.

In summary, one can achieve not only activity foci but also organizing principles (higher level coordination) for those activities. By the introduction of transdisciplinary links between organizational (institution) contexts and scientific (knowledge) activities, a two-level coordination of terms, concepts, and principles results. The contexts move through analysis and its theory, through theory (science) and its strategy, strategy (theory in intervention) and its intervention, and finally, these contexts spiral through interactions back through analysis, theory, and strategy, which results in policy.

Implicit in Fig. 4 and 5 is the dictum commonly heard that vertically organized structures are efficient for solving perceived problems, and loosely coordinated horizontal networks work best for developing scientific inferences and theories. Another dimension might be added — pace-setting events are likely to emerge and be clarified within the public and the politicians beyond the decision-making process and the research network, hence the necessity for advisory councils and citizen participation to interact particularly with the "action-oriented institution." To the extent that the subject matter of Fig. 5 is largely within the domain of the social science disciplines, social science researchers might well mediate between all three: decision makers, researchers, and public advisors.

Emery (1973) makes the point that if social scientists seek only to study the process, they will inevitably influence it; hence they might approach the issue at the outset as one of mediation. But the responsibilities are great, and the process demands an explicit higher-level conceptualization, perhaps a credo, that other actors in the process may recognize and take into account.

Recapitulating, an action-oriented institution will not long remain effective, even if it has mobilized a corps of researchers to attack important questions, unless a loosely coordinated network of robust and relatively independent researchers exists and is accessible, and unless a balanced corps of knowledgeable public advisors makes available its insights to the agency.

Some redundancy will exist, but functional redundancy may be a most important property tending to ensure desirable evolution, relative stability, orderly and manageable response patterns, and a healthy resilience.

Transfer of Science and Technology

Scientific and technical information developed in other countries is transferred to Canada to our advantage (Science Council of Canada Report No. 20). Clearly this is an item of strategic interest and deserves explicit recognition, study, planning, and management. Procedures to oversee and regulate aspects of this process are now developing, and the interests of fisheries deserve fair consideration.

Fisheries conflicts have in the past led to international violence and may do so in the future. The Law of the Sea process is seeking to develop conventions to forestall such events. Perhaps equally important, international organizations of scientists study problems jointly and develop common approaches toward an understanding of difficult problems.

The International Institute of Applied Systems Analysis located at Laxenburg, Austria is a recent creation and joins a large constellation of other international institutions that perform in part a similar function (e.g. FAO, UNESCO, WMO, ICSU, IUCN, etc., plus various derivative groups). Closer to home, numerous Canadians and some Canadian universities are associated with The Institute of Ecology (TIE), an international institute of the Western Hemisphere with headquarters in Madison, Wisconsin. TIE objectives and programs are of particular relevance to strategic planning within Environment Canada, for example.

The number of committees, working parties, seminars, etc., has proliferated to the point that a medium power such as Canada cannot hope to participate effectively in all of them. Whether a screening mechanism could be devised to sort out those of particular interest to Canada should be considered.

Science and technology have long been transferred between nations via published papers and

reports. The generally most effective method is by publication in technical journals that have earned wide respect. Technical journals may be classed into a number of groups: those serving the interests of a small number of closely related scientific viewpoints, those relating to a particular geographic region, those primarily providing an outlet for the work and viewpoints of a particular agency.

Consider the problem of finding an appropriate outlet for fisheries macroecology in a transdisciplinary context, as sketched in this paper. Journals on planning methodology or broad-spectrum scholarly periodicals would be likely outlets, but few fisheries scientists consult such journals. Because this problem existed the *Journal of the Fisheries Research Board of Canada* recently broadened its scope to encompass such articles and to provide a much needed forum for aquatic science. The possibility of broadening other fisheries journals should seriously be considered.

Conventional wisdom holds that researchers, or teams of workers, that are directly responsible to vertical line management can effectively address problems scientifically if the problems are clearly recognized and if standard scientific procedures are applicable. Science as such progresses more rapidly, on average, where the researchers are organized in a loosely coordinated lateral network of persons not subject to the immediate beck and call of the decision-maker or crisis manager. What about the situations that fall between those well-understood extremes: the situations that involve poorly understood crisis problems, and where new methodologies appear to be needed? An aspect of this question was addressed by Regier (1974c) who suggested a division of labor into three groups of scientists: closely directed applied workers, broadly guided or mission-oriented workers, and essentially self-directed researchers.

Limited Mobilization

Ecological researchers and other professionals interested in resources and the environment are gradually being mobilized into more explicit and disciplined institutional structures and problem-solving processes. This is partly a consequence of the success of the ecologists' campaign to inform the public and politicians of ecological concerns, and also of their clamoring for a greater role in planning and decision-making to help rectify past mistakes and prevent future catastrophes. If a crisis threatens we do mobilize and forego some freedom temporarily in order to prevent a more massive and more permanent loss of freedom which would follow if the mobilization did not occur.

But in general the present mobilization appears to be the result of other processes as well, those related to the need to plan for postindustrialism, postconsumerism, postopportunism, etc.

If the more pessimistic ecologists are correct in their assessment of the future, then events will dictate that mobilization will expand and intensify. Clearly this prospect deserves very close study. As with mobilization for war, it seems likely that the first casualties of a crash mobilization process will be conventional freedom and truth. Thus mobilization, even with the best intentions, must be constrained according to clear and acceptable rules.

Creeping, haphazard mobilization is now occurring in a number of ways. Thus researchers within government agencies have in large part been seconded to problem-solving units. In universities, major grants from private and public sources have gone to closely organized or semi-disciplined teams working on priority problems. The Man and the Biosphere Program plans to develop disciplined teams that will include personnel from universities, a number of government agencies, and perhaps private organizations. Among the public, a number of groupings are developing well-organized approaches and are exerting major forces in the broader planning process.

The need to place limits on mobilization of scientific researchers follows in part from the characteristics of the scientific process. The science of today exhibits in general a form of radical agnosticism. Grabow and Heskin (1973) have abstracted one formulation of the current scientific worldview as follows:

> "See Thomas Kuhn's description of the rise and fall of scientific paradigms in his *The Structure of Scientific Revolutions* (1962). He traces the emergence and inevitable disintegration of competing explanations of the perceived universe; the competition for attention among alternate views; the arrival of consensus upon one view; the articulation and extension of that view to cover all perceptions of reality; the emergence of a phenomenon which calls the view into question; and the crises in which alternate views again compete for attention to resolve the anomaly. It is by calling into question the principles of validation by which consensus comes about, as well as articulating the inevitability of the cycle, that Kuhn effects a profound loss of innocence."

Thus mobilization along strict lines may lock workers into a context that may soon be obsolete.

In that they perceive the process of scientific evolution to be gradual, long-term, and perhaps uncontrollable, if they perceive it at all, the great majority of scientists do not explicitly concern themselves about it. They are content to work

within the present time stanza, or the present temporal Gestalt, in which the horizon extends a decade or two into the past and half a decade into the future. But we are now partway into a period of intense transformation, perhaps fairly called a revolution, in which institutions, culture, and science are changing or evolving rapidly. Emery and Trist (1973) predict that this process will continue for several decades. If so, Kuhn's dynamics of scientific paradigms may provide a useful context within which to seek to understand what is happening right now within fisheries science. Rapid evolution may well continue for the foreseeable future.

With respect to limits on mobilization, a recognition of Kuhn's model of paradigm dynamics implies that it is counter-productive to mobilize science too broadly or organize it too closely, unless one's purpose is to defend the frontiers of a personal scientific empire.

In Conclusion

The underlying assumption of the present paper is that intelligent, knowledgeable outgoing people working together cooperatively and democratically within an ordered process in which the rules are explicit and adjustable can resolve some of the problems facing us, to our subsequent long-term advantage. This is the assumption of the entire planning and decision process now building within the government. If this assumption is valid within the present time stanza, it is not clear how long it will remain valid. Presumably the life span of this approach can be shortened or lengthened by our success or failure in applying the process. Adversary battles, power politics, decision by fiat, muddling through with adhockery, are some of the alternatives to collegial planning.

The above paragraph may sound trite to the point of embarrassment. But one of the preeminent rules in rational planning is that assumptions, credos, paradigms, models, etc. be made explicit. Where this rule is not applied, the process fails to be rational.

It is, of course, inconceivable that all research and decision-making will be performed as explicit ordered sequences. As Emery (1973) points out, in any temporal Gestalt some problems are perceived as critical and some of these will be addressed in a most scientific, scholarly way. The great mass of problems perceived as being of minor significance will be dealt with less formally. Some minor issues will blossom into major problems even within the present Gestalt, or may come to be perceived as being of major significance with a change in phase of the culture and the formation of a new Gestalt.

This paper, partially or totally, may be trivial if all that it implies ultimately consists only of an undirected resorting and restructuring of existing components of information, technical competence, insight, theory, disciplines, traditions, and personalities (see Dansereau 1970). A child can build a tower using a set of building blocks at present arranged in the form of a church steeple. The toy tower in itself is no more useful than is the toy steeple. A few scientists do play such games, apparently half consciously, using the work of many other scientists as blocks (or scientists as pawns) for such purposes. The decision-maker will of course seek to guard against initiating exercises that are analogous only to juvenile games. The serious practical objective is to build or rebuild structures and create processes, in science as elsewhere, that are useful for some recognized purpose. It is questions such as these, perhaps in a somewhat broader context, that the Science Council of Canada has been addressing in recent years (Lakoff 1973).

In this paper we have attempted to see into the present — to collect and collate pieces of insight and information on how one might approach the question of what should be the research methodology on major problems with the environment and natural renewable resources such as fisheries. Secondly, given that mobilization of researchers is occurring and will intensify, how might the mobilization be conducted to the long-term advantage of society, science, and scientists.

Formulation of Some Strategic Questions

1. Scientists, in particular fishery ecologists, are being mobilized to deal with problems concerning natural resource exploitation and management, environmental disruptions, consequences of pollution on human health, regional planning, etc. The mobilization is occurring in a disjointed, ad hoc manner, essentially as a series of relatively unordered responses to a mix of crises. The ultimate in ad hoc remedies may be the creation of interdisciplinary teams if it occurs in the absence of prior consensus on higher-level perspectives.

2. Research strategies related to the present mobilization appear to be thoroughly pragmatic:

a) How large should the research budget be?

b) How should the budget be divided among general surveys, resource management, eutrophication, toxic contaminants, assessments of major engineering works, resource development, aquaculture, etc.?

c) How much regional research should be aimed at the Arctic, Great Lakes, Gulf of St. Lawrence, the high seas, etc?

d) How rapidly can changes be initiated in the light of the power structure of the research establishment?

e) What, if any, long-term undertakings concerning support of excellence, either individual or group, now constrain strategic options?

Without challenging the importance of the above questions, this paper addresses the problem of research strategy from a more abstract viewpoint. The hope is that the adversary component in planning will be reduced in importance, and the collegial component increased. Realization of the hope will require that one or more rational contexts be developed.

Following are some strategic questions that relate directly to the conceptual framework sketched in this paper. The ordering is not intended to reflect a priority ranking.

3. Concerning "applied systems analysis":

a) Given that ASA is the preferred format for a problem-solving approach, how rapidly and to what extent should it be stimulated to develop within an agency or institution?

b) Should a formal screening mechanism be developed to identify different levels of problem complexity, only the more difficult to be approached formally as applied systems analyses?

c) Perhaps as an aspect of screening, how can the important properties "scale and scope" be identified and clarified objectively?

4. Concerning disciplines:

a) Should the approach to multidisciplinary research and problem solving be formalized beyond the degree to which this occurs within applied systems analyses undertaken ad hoc on important issues?

b) Should special encouragement be offered to ongoing efforts to identify and clarify conceptual isomorphisms, among the disciplines of particular interest to an agency, in order to improve the efficiency of multidisciplinary work?

c) Should universities be encouraged in their attempts to reorganize parts of their disciplinary framework, and should an environmental macrodiscipline be explicitly encouraged to develop?

d) Are the "transdisciplinary foci" herein proposed useful for guiding selection of members for interdisciplinary teams so that some specialization may be induced?

5. Concerning technical sophistication:

a) As the demands for particular kinds of technical, quantitative sophistication evolve, should a formal mechanism be developed to stimulate and direct the evolution?

b) In order to direct the appropriate technical quantitative competence to the various demands of different problems, can competence and problem characteristics be analyzed into mutually congruent sets (see 4d above)?

c) Should the various traditions, within that science which is generally accepted to have some relevance, be assessed objectively for their possible future contributions, and supported in the light of such an analysis?

6. Concerning institutional structures and interactions:

a) Should the structure and dynamics of interactions between a government agency, universities, advisory bodies, plus other nongovernmental organizations be analyzed from the viewpoint of the consideration that the general planning and decision-making process can become more efficient through consensus on a division of labor?

b) How can the transfer of science and technology be ordered within and between nations to be usefully effective yet not swamp a nation's scientific corps?

c) Would it be useful to classify an agency's scientists into three groups with somewhat different duties, related to the need for undirected, mission-oriented, and program-dictated research?

d) How should the vertically organized problem-solving scientific corps, including mission-oriented plus program-dictated researchers be interfaced with the laterally coordinated theory-seeking scientific corps, including undirected researchers plus many workers in universities?

7. Concerning mobilization:

a) Given that mobilization is occurring and will likely intensify, what safeguards will prevent excessive sacrifices of "truth and freedom"?

b) By what criteria can an agency or institution know that proposed conceptual frameworks, mobilization schemes, perceptions of pending crises, etc., will be useful in practice for the "foreseeable future"?

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Conceptual Aspects of Strategic Planning for Fishery Management and Development

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The decision-making component of the process is supported by mechanisms to provide for continuous adjustment of planning and adaptation to an evolving environment. These include a) formally organized input from clients, b) "feedback" in the form of goal-attainment indicators or quantitative/qualitative measures of social and industrial changes and of program impact, and c) policy research or analysis directed to minimization of the intuitive element in decision making.

Planning is conceived to be an integrated process combining a) definition of goals and establishment of priorities or policy objectives, essentially a political activity, b) selection of policies or strategies for the achievement of indicated objectives and the establishment of guidelines for programming, based on interaction between political leadership and expert advisers, and c) selection of programs and project design, i.e. tactical or operational planning, a specialist activity.

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Le composant prise de décision du processus de planification stratégique s'appuie sur des mécanismes qui prévoient un ajustement constant de la planification et une adaptation à un milieu en évolution. Ces mécanismes comprennent: a) apport formellement organisé des clients, b) «feedback» sous forme d'indicateurs des buts atteints, ou mesures quantitatives/qualitatives des changements sociaux et industriels et de l'impact des programmes, et c) recherches sur les politiques ou analyse visant à minimiser l'élément intuition dans le processus de prise de décision.

On conçoit la planification comme un processus intégré combinant: a) définition des buts et établissement des priorités ou objectifs des politiques, essentiellement une activité politique, b) choix des politiques ou stratégies en vue d'atteindre les objectifs indiqués et établissement de règles directrices pour la programmation, basés sur l'interaction entre la direction politique et les aviseurs experts, et c) choix des programmes et préparation des projets, i.e. planification tactique ou opérationnelle, domaine des spécialistes.

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THE development hitherto of policy for fisheries management has been unsatisfactory for a variety of reasons, the most important of which is the involvement of decision-makers with program planning exclusively. Lacking a long-range perspective the approach has tended to be disjointedly incremental, with objectives being inferred from existing activities. The intention in the present paper is to delineate an appropriate conceptual framework for a systematic approach to planning and policy development.

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Strategy vs. Tactics

Dissatisfaction with decision-making performance up to the present, in the fields of fishery management and development, is attributable to a number of causes. "The Major Problem...lies in decision-making institutions, and the major problem in institutional development is that of developing an institutional strategy. This is not a fishery problem *per se*...(it) is (a) general...problem..." (Rothschild 1973, p. 2026). Resistance to fundamental change commonly is deep-rooted and pervasive. Organizational change ("the multiplication of structural units, the nice elaboration of functional

charts and the conferring of imposing titles") as a substitute for change in substance, is said to be a typical disease of bureaucracies.

The administrative world, it is alleged, is peopled with an excessive number of "ostriches" and "dinosaurs," the former with their heads buried in the sands of bureaucratic fantasy and the latter basking in the memory of past achievements, and both lacking "...one of the most important virtues of an administrator...the ability to understand rapid and complex environmental changes and ...adapt creatively to (them)..." (Rothschild 1973, p. 2026). In conditions of this kind, planning, if indulged in at all, becomes merely "ritualistic."

More specifically, some important sources of weakness in past decision-making processes have been identified as follows: a) a tendency to be preoccupied with tactics to the detriment of strategy — "...if tactical, non-responsible decision-making tends, in the absence of a strategic framework, to dominate the...process,...this may be called irresponsible decision-making." (Rothschild 1973, p. 2027); b) a failure to understand the complex interrelationships among the problems dealt with and to comprehend the nature and characteristics of the total system — "If the complexity of the fishery system is not acknowledged, this will lead to suboptimization whereby one element (e.g. the design and location of a processing plant)... may be optimized but the total system (including, for example, the resource base) is ignored..." (Rothschild 1973, p. 2028); c) a failure to select and concentrate on the best set from among a variety of alternative courses of action — "Many national planning...documents are tragic monuments of failure in strategic selectivity. Too often they are built on the double principle of 1) stringing together separate plans or programs emanating from every major (management centre)... or 2) providing something for every active pressure group and region. This 'laundry list' planning sometimes approaches sheer irresponsibility." (Rothschild 1973, p. 2028); d) a related tendency to adopt a disjointed, incremental approach to decision-making, without reference to a long-range general model — "Experience has shown that public expenditures can become self-justifying, that is, instead of assessing their results in the light of previously established objectives and intended results, the objective is inferred from the actual results..." (Economic Council of Canada 1971, p. 32) and "To treat means as ends seriously restricts the range of options available for reaching the 'true' ends... (it is valid, however) to identify what might be termed 'derivative goals' as long as it...(is) clear that their pursuit...(is) desirable only when this...(is) the most effective means of achieving more ultimate ends..." (D. G. Hartle unpublished data); e) a failure to recognize conflict as the essence of administrative problems — "Owing to the tactical nature of (the approach)...it tends to ignore the identification of the parties at conflict and (to appraise)...their strengths and their interests, both apparent and actual, as well as to evaluate the various conflict outcomes: avoidance, deadlock, defeat or victory, compromise and integration..." (Rothschild 1973, p. 2028); f) a failure to appreciate the need for a sequential, iterative process in model building, the builder interacting with the user to produce a dynamic, rather than static, model — "The main point...is that model building is a scientific endeavour but model using is an activity employed by decision-makers. Because the model builder often has different objectives than the model user...the models which are produced...(if usually interesting) are not necessarily useful." (Rothschild 1973, p. 2028)

It would be reckless to claim that the federal administration of fisheries in Canada has always been free from defects like these.

Strategic Decision-Making

An essential requirement for efficient decision-making is a firm conceptual basis, an accurate knowledge and understanding of the contemporary and probable future environments in which this activity is exercised. First of all, the real world is characterized by great and increasing complexity. Salient features of this world (representing opportunities as well as problems) are (Rothschild 1973, p. 2020): a) mounting economic and social stress, e.g. emerging crises in international trade and monetary arrangements and dispairing reaction to the inflation/unemployment trade-off;

b) growing environmental uncertainty, e.g. rapid and unpredictable change in human aspirations, social structures, and coalitions of political power;

c) increasing structural intricacy, e.g. greater specialization, larger organizations and more labyrinthine interrelationships within and among organizations;

d) more "performance" complexity, i.e. necessarily conflicting criteria governing organizational activity over large expanses of space and time and cultural and psychic distances;

e) uneven technological change: dramatic leaps forward in some areas, e.g. the armament and space industries, and comparative backwardness or stagnation in others, e.g. some small-boat fisheries;

f) the unsettling effects of such change, i.e. the undermining of the status and power of people accustomed to traditional ways of life;

g) the obsolescence of yesterday's innovators, i.e. the increasing irrelevance for the future of the analytical and managerial techniques so far perfected;

h) the spreading fallacy of administration as gadgetry, i.e. the application of "...specialized techniques of analysis or control, mistakenly viewed (or fraudulently advertised) as substitutes for genuine managerial wisdom, judgement and... more profound...approaches," e.g. Program Planning and Budgeting or Management by Objectives.

Efficient techniques for optimal choice among alternative policy goals or objectives, and among strategies for the attainment of those goals, must be perfected. Distinctions between short-run and long-run advantage, for example, and between economic growth and social welfare, require evaluation — and so on. For this purpose, a holistic approach is necessary, i.e. the fisheries must be regarded as a "system" embracing all the "linkages" between the natural resources and man's use of them. The linkages involve biological, economic, social, and political components, no one of which is necessarily of greater importance than another.

Management and development objectives of a biological, an economic, a social, or a political nature are complicated in themselves and the interrelationships among them are even more so. An attempt to optimize an objective or objectives in one such field would be totally unrealistic. Problems in fishery management and development, therefore, must be studied in a systematic way.

The approach is iterative and, accompanied by genuinely interdisciplinary research, permits the unravelling of what at the start may appear to be insuperable complications.

"The fundamental problem of fishery development might very well be the mobilization and allocation of financial and intellectual resources to the solution of natural-resource problems, which by definition involves the development of algorithms or rules for making the right decisions. The inefficient mobilization or (the) misallocation (of such resources)...are evident in many circumstances: for example, when a fishery is managed as a single species fishery when it catches several species. Another example is when the total disciplinary spectrum is not considered, for instance, the economic aspects but not the biological...or vice versa. An even more insidious misallocation of talent is the paying of lip service to being multidisciplinary...Being only nominally multidisciplinary will not produce results of multidisciplinary utility..." (Rothschild 1973, p. 2021).

The strategic decision-maker, then, is responsible for a) dealing directly with changing patterns among multiple objectives, b) handling all relevant variables, including those that are incommensurable, c) understanding that, in the matrix of decision-making, his decisions may conflict with those of others, d) realizing that each decision made changes the environment for subsequent decision-making, e) innovating norms for the elucidation of problems previously overlooked or ignored, f) subordinating (without neglecting) short-term considerations of feasibility to long-term considerations of desirability, and g) generating appropriate forms for the tactical approach to programming. (Rothschild 1973, p. 2027).

Beyond that, of course, the repertoire of strategic decision-making includes (as well as the objective activity of transmitting information, for example) activities that are directed a) to the awakening and organization of interests in support of policy initiatives and b) to evoking action for particular ends through various modes of persuasion or influence. These, however, are the responsibility of political leadership. On this point, the Economic Council of Canada (1971, p. 32) has said that:

"Political reality has to accommodate many values and interests, and negotiation among them must determine social objectives.

In order to bring policy to the point of implementation, politicians frequently need to obtain support inside or outside the legislature by consensus or coalitions; this may require the selection of less efficient or effective policies and programs. This bending to reality is part and parcel of the system. If a policy that is 'technically best' is politically unacceptable, it is irrelevant and some other must be sought."

"Today's policy design is directed toward the future, but social change is proceeding at a rate that threatens to render obsolete the traditional and mechanistic methods of anticipating what that future will be."

"Many problems and policies need a long-term view, but the time horizon of legislative bodies is, by and large, relatively short."

In a democracy, the people's views are transmitted through special-interest groups (lobbies, etc.), as well as through their elected representatives, and, in recent years, the number of such groups, representing a variety of initiatives, has proliferated. This increase in organized opinion is advantageous

for policy-formation, provided that citizens are enabled to analyze policies critically and constructively. As it is, however, the general public often may be ill-informed (or misinformed), even after the fact, about the considerations underlying government decisions. In some circumstances, the consequence can be advocacy of dangerously simplistic solutions to what are in fact extremely complex problems (Economic Council of Canada 1971, p. 84–85).

"It would be difficult to prove that the occasional 'sound and fury' of collective response to public issues implies larger or wider citizen participation than in less noisy days. Nevertheless, groups representing (various social elements)...are pressing for increased involvement in public policy-making. These developments are raising new questions about how to maintain the essential elements of a democratic system in an increasingly vocal and pluralistic world." (Economic Council of Canada 1971, p. 230)

Planning and Policy Development

This paper is not concerned with the institutional aspects of decision-making, i.e. the "structure" or network of organizations and individuals contributing inputs to the policy-making process. Assuming that fisheries are to be considered a broadly-based system, it follows that an approach to policy-making for the fisheries should be similarly broad. For this purpose, there is unlikely to be an uniquely ideal or optimal structure. As the Economic Council (1971, p. 33 and 63) has put it,

"While it would be infinitely simpler, public decisions should not arise 'phoenix-like' from a single monolithic hierarchy. They should be generated by exchanges among interested and responsible participants reflecting the need for policy formation to contain different values, interests and disciplines. ...decision-making is essentially a process of choosing among alternatives; in order to make appropriate choices, it is essential to use the widest possible basis of relevant information and to apply the best possible analytical techniques; and the process must be one that avoids the dangers of bureaucratic and technocratic dominance by providing increased "openness" in government decision-making."

A simplified flow-diagram of the central part of the decision-making process is shown in Fig. 1. It focuses on certain key features of the process: a) selection of alternatives at the levels of

i) goals or objectives (mainly political activity)
ii) policies or strategies (mixed politician/expert interaction)
iii) programs or tactics (mainly technical-specialist activity)

b) analysis, c) feedback from operations, d) monitoring of program impacts.

As suggested earlier, there has been a tendency hitherto to concentrate on the third level of decision-making, that of program design and implementation or tactics. This is the level at which operational questions are dealt with, e.g. estimation of resource requirements and allocation of funds. It is also the level at which outcomes should be anticipated and actual results evaluated and, for that reason, it is an integral element in the feedback loop. Apart from that, however, attention in the present paper is directed to the other levels of decision-making, those of goal-setting and strategy proper, and to the other elements of the total process.

At the highest level of the decision-making process, the "grand design" of national goals and priorities is formulated. Goal priorities, i.e. policy objectives, are selected from a wide variety of public concerns. These objectives are in the form of "general statements of intent directed towards achievement in particular goal areas" (Economic Council of Canada 1971, p. 66) sufficiently specific to be operationally relevant.

"Goals that seem reasonable, desirable and universally acceptable are almost invariably too general to provide an adequate basis for policy. As the specification of general goals into detailed objectives begins, the controversy about interpretation arises. The conflict of interest that is at the heart of the political system extends beyond the problem of elaborating the goal to everyone's or no one's satisfaction; it involves choosing among alternative goals and establishing time preferences." (Economic Council of Canada 1971, p. 67).

At any point in time, public concern is likely to be fixed on a limited number of issues. The decision-making process, however, potentially extends across the whole spectrum of public interest and welfare and, to provide for concerns as yet unperceived, the framework must be open-ended. Time is a critical variable in the decision equation. Today's choice and ranking of objectives affecting future action, is based largely on information about the past. There are lags in perceiving problems, in responding to them and in effecting change. The choice of policy objectives and success in meeting them require a long-range perspective, only to be attained by continuous monitoring of social change (Economic Council of Canada 1971,

p. 70) — hence the significance of the informational bases of decision-making, such as the goal indicators discussed farther on.

Policy objectives having been established the process moves to the implementation of objectives, i.e. the selection of policy options or broad guidelines (strategies) for action. Decisions at this level also may depend wholly or partly on a (political) value assessment. The critical questions surrounding a decision on strategy, or on a combination of strategies, relate to the identity of the group or groups affected and to its or their characteristics. The choice of a strategy is unlikely to be of an "either/or" type: an effective attack on a problem in most cases requires a mix of actions, the weight placed on each determining the general "thrust" adopted.

The essence of policy-making is the selection and combination of strategies aimed at meeting objectives, while considering the widest possible range of alternatives. At some point, the benefits to be obtained from finding an optimum are likely to be outweighed by the costs of further search for alternatives. An important element in such costs is the time factor: delay in reaching and implementing a decision may give rise to a reaction on the part of the public that would impede effective policy application. Judgement, the quality of wisdom and experience, is thus the crucial element at this as at other stages of the decision-making process: judgement as to the alternatives to be considered, the interrelationships to be examined, and the extent to which analyses are to be pursued. Neither simple nor complex formulas can replace this quality and alone generate creative and imaginative responses in the process (Economic Council of Canada 1971, p. 79).

"One of the most important aspects or phases of the policy-making process is strategy, which sets guidelines and assumptions for policy-making that reflect a type of 'grand plan' clearly distinguishable from the lower and tactical levels of decision-making. The dimensions of strategy cover broad and general questions such as: the problem of choosing single or multiple strategies; the degree of policy change — marginal and incremental or total and innovative; the time horizon of policy — short- or long-term; the time preference which, contrary to normal practice, may, in some instances, value the future above the present; the use of alternative strategies to take account of problems of uncertainty and risk; and the use of a 'best attainable' solution when

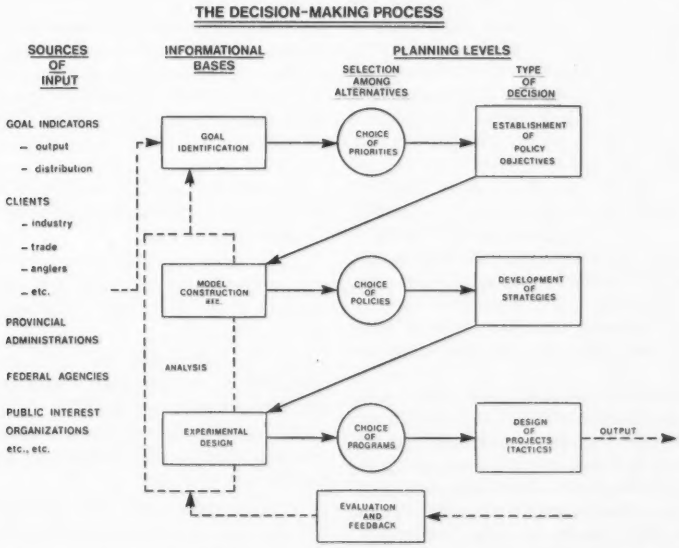


FIG. 1. Adapted from Economic Council of Canada 1971, p. 65. The system is very much condensed; it does not incorporate all elements or illustrate fully the complexity of the flows. In practice, moreover, decisions rarely would be made sequentially as indicated; rather than being discrete, the three levels of decision-making shade into each other.

a 'technically best' solution is not feasible." (Economic Council of Canada 1971, p. 32)

The distinction between decision-making at the strategic and tactical levels has been described (Rothschild 1973, p. 2025) in the following terms.

Strategy	Tactics
Relatively broad in scope	Relatively narrow in scope
Relatively long time horizon	Relatively short time horizon
Defines problems	Seeks objective solution to problems as defined
Considers relationships with other problems	Considers only solution of particular problem
Concentrates on desirability	Concentrates on feasibility and consistency
Systems-analysis oriented	Operations-research oriented

To illustrate the difference by reference to the fisheries, it may be said that optimization in the allocation (use) of society's resources is a policy objective (goal priority), rationalization of the fishing industry (to that end) is a strategy, and institution of entry-control in particular fisheries (for that purpose) is a tactic.

The analytic component of the decision-making process, embraces not only systems analysis but, ultimately, all relevant research disciplines. In many respects, especially those relating to behavioral response and motivation, knowledge of the segment of society associated with the fisheries, for example, and insight into the impact of alternative strategies upon it, is meager. The construction of models, the design of experiments and of evaluation techniques, all directed to the realignment of policy objectives and strategies as necessary, involve a commitment to the extension of knowledge and information on a broad front.

Similarly, operations research and benefit/cost analysis are some of the analytical techniques directed to a deeper understanding of tactical devices, i.e. the design and evaluation of program and project alternatives, the purpose being appraisal of the real (as well as the financial) costs and benefits of programs in the context of policy objectives. Analysis at this level must also take account of interrelationships and "spillover" effects, knowledge about which is desirable as a basis for the design of program networks in which such effects reinforce rather than impede progress toward objectives. (Economic Council of Canada 1971, p. 1–81).

"Some may suggest that (such) articulation is impossible or unnecessary. But governments propose acts which, in the absence of such knowledge, must rely on traditional views, hunch or guess-work. In many instances, particularly those relating to social policy, the behavioral relationships are too complex for intuitive judgements. While the factual content of public policy may not be the main or ultimate criterion of many public decisions, it can scarcely be doubted that more knowledge about how the system works would lead to better decisions."

"There is, of course, an important element of judgement here too. At some depth of analysis, almost everything can be seen to relate to everything else; at that point the analysis sinks under its own weight..."

Techniques of evaluation, applied at the tactical or programming level to determine the efficiency with which resources are being used in specific projects, have been elaborated fairly extensively in the recent period (D. G. Hartle unpublished data). In the present instance, in relation to the clarification of strategic issues, attention is directed to appraising the relevance or effectiveness of programs and projects in relation to policy objectives. In the decision-making process visualized, a feedback loop from continuous program evaluation into analysis and policy formulation is a crucial element.

"Evaluation (both retrospective and prospective) is...one of five elements of...strategic planning. These elements are:

1. forecasts of the changes in the indicators of goal achievement that would occur in the absence of changes in the policy instruments (expenditure programs, etc.);

2. the assignment by Ministers of priorities to the present or emerging problems identified on the basis of this information;

3. identification of the kinds of policy-instrument changes that might be used to meet these high-priority problems;

4. assessment of their relative effectiveness, taking into account any positive or negative effects on other goals...;

5. Selection by Ministers of the changes in the policy instruments that would most effectively resolve the highest priority problems of the Government.

Evaluative and strategic planning are...inextricably related. Evaluation proceeds from the policy instruments to their effects on goals. Strategic planning proceeds from the desired attainment of goals to the selection of the mix of policy instruments best able to achieve them, using the information produced through evaluation." (D. G. Hartle unpublished data)

In practice, policy objectives are selected in conditions of change and uncertainty and under the constraint of limited technical and financial resources. An appraisal of problems not only as they exist in the present but as they may develop in the future is required. An assessment of prospective gains from increments of expenditure and of possible trade-offs is necessary. An important function of feedback at this level is to confirm the tentative nature of objectives by providing for their reassessment in the light of increased knowledge and environmental change. When the results are contrary to what is expected or intended, the decision-maker is given an opportunity to adapt or revise policies and programs.

"The life of a decision-maker would certainly be a great deal easier, though perhaps far less stimulating, if society were static and unchanging. But it is not. Rather, society is constantly changing, partly as a result of decisions made by governments. In these circumstances, there is no guarantee that the anticipated or designated outcome of particular policies or programs will be attained, no matter how well designed they may be. What is required is a systematic way of learning from experience that will bridge the gap between today and tomorrow." (Economic Council of Canada 1972, p. 81)

A basic source of input to the process of policy formulation is provided by so-called "goal indicators," i.e. indicators of goal attainment or achievement. These are defined as "quantitative–qualitative information that can be collected on a time-series basis to measure a relevant and significant dimension of a specified goal area." (Economic Council of Canada 1972, p. 71) In many goal areas, the available information is inadequate to answer some of the simplest, but fundamental, questions.

"The goal areas include interests and concerns of both individuals and governments. In Canada, private decisions still govern a large share of total activity. For private industry, the market mechanism, even with its imperfections, provides some insight into 'revealed' preferences, as well as guidance for resource allocation.

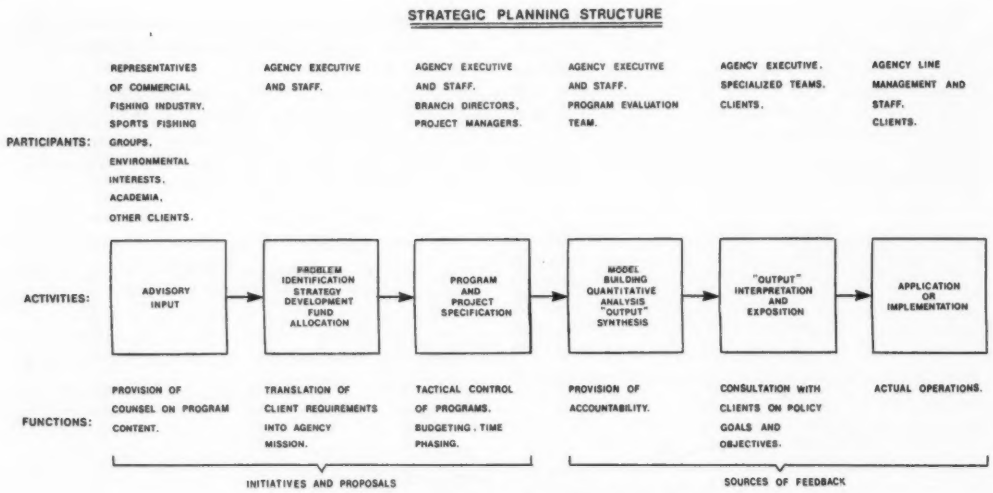
The government sector, on the other hand, enjoys no comparable self-regulatory machinery. What is needed are more and better signposts along the route that society is following." (Economic Council of Canada 1972, p. 70–71)

"Perhaps the most intractable problem in implementing...(a) system of policy evaluation and strategic planning...is that encountered in trying to reach agreement on operational definitions of those Government goals which are conceivably quantifiable. The field is strewn with ideological and semantic pitfalls. But unless agreement can be reached on...goals that can be defined operationally — that is to say in a manner that makes it possible to assess objectively the degree to which they are being realized — analytical techniques which could make a significant contribution to the decision-making process lose their value. There is no doubt that it is next to impossible to define some perfectly legitimate goals operationally...while one would expect that the subjective evaluation of Ministers will always play the dominant role in assessing the degree of goal attainment in cases such as this, the basic argument...is that there are many goals that can and should be defined operationally and measured, at least in part, statistically..." (D. G. Hartle unpublished data)

It is pointed out that, in the past, major policy changes have tended to be adopted in response to dramatic events, i.e. that a situation may have to develop critical proportions before it looms large enough to obtain the level of visibility that attracts public awareness and involvement. Continuous monitoring of social conditions could render the trend of events more "visible," generate warranted concern and provide a foundation for appropriate and timely action before problems become crises.

In the absence of such "early warning" intelligence, priorities become dependent on "ad hocery" and objectives may lack relevance. Ideally, goal indicators would reflect society as in a mirror and permit objectives being developed in response to perceived need — and, on the basis of such objectives, realistic strategies being evolved and programs designed. Program initiatives, however, are aimed at changing some aspect of society. If realized, the change is reflected subsequently in the indicators, stimulating reassessment and, when necessary, realignment of objectives, strategies and programs (Economic Council of Canada 1972).

It is recommended (Economic Council of Canada 1972, p. 71–72) that for each goal area there should


STRATEGIC PLANNING STRUCTURE
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REPRESENTATIVES OF COMMERCIAL FISHING INDUSTRY. SPORTS FISHING GROUPS. ENVIRONMENTAL INTERESTS. ACADEMIA. OTHER CLIENTS.
AGENCY EXECUTIVE AND STAFF.
AGENCY EXECUTIVE AND STAFF. BRANCH DIRECTORS. PROJECT MANAGERS.
AGENCY EXECUTIVE AND STAFF. PROGRAM EVALUATION TEAM.
AGENCY EXECUTIVE. SPECIALIZED TEAMS. CLIENTS.
AGENCY LINE MANAGEMENT AND STAFF. CLIENTS.
ACTIVITIES:
ADVISORY INPUT
PROBLEM IDENTIFICATION STRATEGY DEVELOPMENT FUND ALLOCATION
PROGRAM AND PROJECT SPECIFICATION
MODEL BUILDING QUANTITATIVE ANALYSIS "OUTPUT" SYNTHESIS
"OUTPUT" INTERPRETATION AND EXPOSITION
APPLICATION OR IMPLEMENTATION
FUNCTIONS:
PROVISION OF COUNSEL ON PROGRAM CONTENT.
TRANSLATION OF CLIENT REQUIREMENTS INTO AGENCY MISSION.
TACTICAL CONTROL OF PROGRAMS. BUDGETING. TIME PHASING.
PROVISION OF ACCOUNTABILITY.
CONSULTATION WITH CLIENTS ON POLICY GOALS AND OBJECTIVES.
ACTUAL OPERATIONS.
INITIATIVES AND PROPOSALS
SOURCES OF FEEDBACK

FIG. 2. Adapted from Rothschild 1973, p. 2027.

be indicators of two types: output indicators and distribution indicators. The first type is intended to measure the level of and changes in the real "output" of a system. In the short run, since a conceptual basis for the measurement of real output is lacking in many cases, provisional substitutes or "proxy" measures may be used (cautiously) as a guide for decision-making.

The second type of indicator, intended to show the distribution of the aggregate output among regions, groups and so forth, is required for exploration of fiscal equity in government programs, i.e. "the net balance of two vital questions: Who pays? Who benefits?" Apart from the intentional impact of policies and programs directed at specific groups of the population, many policies and programs have a distributional impact that is a side effect or spin-off from action to accomplish other ends. Such effects are not uncommon and they may be massive and knowledge of them is of great importance to decision-makers at both the policy development and the programming levels of the process.

It is suggested (Economic Council of Canada 1972, p. 74–75) that goal indicators should be relatively few in number for each goal area and that they should provide a broad, summary picture of the area of concern. They should take the form of statistical time series that would indicate the state of the area at regular time intervals, depending largely on the rate of change in the area under observation. One such indicator, to fill a gap in data on the fisheries system, might be an index of (gross and/or net) income to individuals from fishing.

This completes the outline of a decision-making process with particular reference to the strategic-planning component. A variant schema is provided in Fig. 2. The discussion has concentrated on the way in which decisions are, or should be, made. Consideration of the decision-makers themselves has been eschewed but the Economic Council, from whom so much of the substance of this paper has been drawn, may be permitted a final word on the subject:

"We emphasize in the strongest possible terms that progress towards improved government decision-making is *not* simply a matter of developing better information and adopting new and more sophisticated techniques. Increasingly sophisticated as they may become, better information and techniques are only aids for improving judgement. Decision-making is essentially a judgemental process. What really matters is the approach to thinking about the choices that need to be made — a continuous, conscious and deliberate weighing of alternative actions on the broadest possible basis of knowledge and participation..." (Economic Council of Canada 1972, p. 64).

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Recent Studies on Investigations Published in Other Periodicals

Until 1970, reprints of these articles had been included in an annual volume of "Studies," composed of two parts. The final binding was the 1969 Studies, Part 2, which included No. 1355. These are no longer bound and distributed. We continue, however, to number and list all articles, which henceforth may be obtained in reprint form only from the author or originating establishment.

Récentes études sur des recherches mentionnées dans d'autres périodiques

Jusqu'en 1970, ces articles étaient réimprimés, puis reliés dans un volume annuel d'études, comprenant deux parties. Les études de 1969, partie 2, incluant le n° 1355, ont été les dernières à être reliées. Nous n'en faisons désormais plus la reliure ni la distribution. Nous continuons cependant de numéroter les articles et d'en établir des listes. On peut donc se les procurer, sous leur forme réimprimée seulement, de l'auteur ou du service dépositaire.

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1968. PARSONS, L. S. 1972. Use of meristic characters and a discriminant function for classifying spring- and autumn-spawning Atlantic herring. Int. Comm. Northwest Atl. Fish. Res. Bull. 9: 5–9. (9)

1969. CARROTHERS, P. J. G., AND T. J. FOULKES. 1972. Measured towing characteristics of Canadian east coast otter trawls. Int. Comm. Northwest Atl. Fish. Res. Bull. 9: 11–19. (6)

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1971. HALLIDAY, R. G. 1972. The fishery on the southern Gulf of St. Lawrence cod stock, 1960–70. Int. Comm. Northwest Atl. Fish. Res. Bull. 9: 51–64. (6)

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Interpretive Articles Series

This new series commenced in 1966. The articles interpret work already published in primary journals. They appear at irregular intervals in various technical publications. Frequently an article essentially duplicates, condenses, or is based on an article in another series.

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307. RAZZELL, W. E. 1974. Progress and projections. Fish. Mar. Serv., Vancouver Lab., Vancouver, B.C. 21 p. (2)

308. BERNARD, F. R. 1974. Book review of: Sea shells of tropical west America; marine mollusks from Baja California to Peru, 2nd ed., by A. M. Keen, with the assistance of J. H. McLean. Stanford University Press, Stanford, Calif. J. Paleontol. 48: 202 (1)

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312. WALDICHUK, M. 1973. Report of the relationship of GIPME to GEMSAMP. UNESCO, Paris, France. 6 p. (3)

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314. WALDICHUK, M. 1973. International approach to the marine pollution problem. Ocean Manage. 1(1973): 211–261. (3)

315. WALDICHUK, M. 1973. Conference report. FAO (U.N. Food Agric. Org.) Technical Conference on Fishery Management and Development, Vancouver, B.C., Feb. 13–23, 1973. Ocean Manage. 1(1973): 201–218. (3)

Manuscript Report Series

This series includes unpublished preliminary reports and data records not intended for general distribution. They should not be referred to in publications without clearance from the issuing establishment and without clear indication of their manuscript status.

Rapports manuscrits

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PARKER, R. R., J. SIBERT, AND B. A. KASK. 1973. Density of bacterial colonies in relation to the distribution of salinity and of pulpmill effluent in Alberni Inlet, B.C. Fish. Res. Board Can. MS Rep. 1274: 107 p. (1)

RESEARCH AND DEVELOPMENT, FISHERIES AND MARINE SERVICE, NANAIMO, B. C. 1973. A discussion of the impact of the proposed Nanaimo Harbour development on the aquatic environment and its fishery resources. Fish. Res. Board Can. MS Rep. 1275: 27 p. (1)

LEE, J. C., AND N. BOURNE. 1973. Marine bibliographical and review study of Pacific Rim National Park. Fish. Res. Board Can. MS Rep. 1276: 121 p. (1)

BUSTARD, D. R. 1973. Some aspects of the winter ecology of juvenile salmonids with reference to possible habitat alteration by logging in Carnation Creek, Vancouver Island. Fish. Res. Board Can. MS Rep. 1277: 85 p. (1)

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STEPHENS, K. 1973. Data record. Primary productivity data from Nanaimo River estuary for 1973. Fish. Res. Board Can. MS Rep. 1280: 29 p. (1)

WHITE, A. W., AND H. M. AKAGI. 1974. A compilation of total releases and recoveries of drift bottles and sea-bed drifters in continental shelf waters of the Canadian Atlantic coast from 1960 through 1973. Fish. Res. Board Can. MS Rep. 1281: 49 p. (6)

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HOURSTON, A. S. 1973. Preliminary analysis of British Columbia herring stocks in 1973 and forecasts for 1974. Fish. Res. Board Can. MS Rep. 1285: 23 p. (1)

SMITH, M. S. 1974. Halibut incidence in trawl catches of the *G. B. Reed*, September 1973. Fish. Res. Board MS Rep. 1286: 5 p. (1)

MESSIEH, S. N. 1974. Surface and bottom current-in the Gulf of St. Lawrence, as inferred from res coveries of drift-bottles and sea-bed drifters released in 1967–68. Fish. Res. Board Can. MS Rep. 1287: 25 p. (6)

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SMITH, M. S. 1974. *A. P. Knight* groundfish cruise no. 73–2, October 22–30, 1973. Fish. Res. Board Can. MS Rep. 1290: 17 p. (1)

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VARIOUS AUTHORS. 1974. Summary of physical, biological, socio-economic and other factors relevant to potential oil spills in the Passamaquoddy region of the Bay of Fundy. Fish. Res. Board Can. Tech. Rep. 428: 229 p. (7)

MILLER, R. J., AND J. R. HOYLES. 1973. Loss of commercial snow crabs to cod gillnets in Newfoundland. Fish. Res. Board Can. Tech. Rep. 429: 21 p. (9)

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LEVINGS, C. D., AND N. G. MCDANIEL. 1974. A unique collection of baseline biological data: benthic invertebrates from an underwater cable across the Strait of Georgia. Fish. Res. Board Can. Tech. Rep. 441: 19 p. (3)

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PARKER, R. R., R. MACKENZIE-GRIEVE, AND B. A. KASK. 1974. The distribution of chemical properties in the waters of Alberni Inlet, B.C. in 1971: an atlas. Fish. Res. Board Can. Tech. Rep. 444: 43 p. (1)

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PECHKURENKOV, V. L., I. A. SHEKHANOVA, AND I. G. TELYSHEVA. 1972. Results of research on the research of chronic exposure to various concentrations of radionuclides on the embryogenesis of fish. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn Khoz. Okeanogr. 85: 9–26. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2967, 1974) (9)

YUKHIMENKO, S. S. 1972. Parasitic fauna of silver carp *Hypophthalmichthys molitrix* (Val.), and grass carp *Ctenopharyngodon idella* (Val.) in the Amur River. Izv. Tikhookean Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. (TINRO) 77: 151–159. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2968, 1974) (1)

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POLENOV, A. L., I. V. YAKOVLEVA, AND P. E. GARLOV. 1972. Ecological, histological and experimental analyses of the neurohypophysis and thyroid gland in acipenserids under conditions of extreme stress, p. 263–282. *In* Acipenserids and problems of their culture. Pishchevaya Promyshlennost, Moscow. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2975, 1974) (8)

PICCINETTI, C. 1967. Diffusion of the carcinogenic hydrocarbon benzo 3–4 pyrene in the upper and middle Adriatic Sea. Arch. Oceanogr. Limnol. 15: 169–183. (Transl. from Italian by Fish. Res. Board Can. Transl. Ser. No. 2976, 1974) (3)

TSUKERZIS, Y. M., AND I. A. SHESTOKAS. 1967. Crayfish resources and ways to increase them in the lakes of northeastern Lithuania. Tr. Karel. Otd. Gos. 5: 211–218. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2977, 1974) (4)

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Journal Fisheries Research Board Canada

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A more detailed guide on preparation of manuscripts from theses is available from the Office of the Editor.

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The *Style Manual for Biological Journals* (3rd ed. American Institute of Biological Sciences, 3900 Wisconsin Ave. NW., Washington, D.C.) is used as the authority in matters of form. The standards for spelling are: *Webster's Third New International Dictionary* and *le Grand Larousse Encyclopédique*. Titles of periodicals are abbreviated as in the *Biological Abstracts* list. References to literature are made by the name-and-year system. The *Journal* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (Third Edition, 1970) Special Publication No. 6 of the American Fisheries Society.

Notes are distinguished from *papers* on the basis of scope or completeness, rather than quality, of the research. They may be on problems with narrow, readily defined limits; on work that is largely confirmatory; on fishing gear or methods, or research techniques; on advances in knowledge arising as by-products of broader studies; on progress in projects that were discontinued; or on preliminary findings that warrant publication before problems are resolved. They may be organized with as much flexibility as papers except that they may have no centered headings. They should take no more than four pages in the *Journal*.

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Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables or figures and the text, or within the text? Should some of the data be made available separately, in a manuscript report or at a data repository? If you use statistical analysis are the statistics subordinate to the biology?

Would any of the text be clearer if condensed? Are summary statements given at the beginnings of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the *title* encompass the content of the report?

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Is the *introduction* largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem?

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Are generalizations on the *results* adequate? Are findings distinguished from inferences from them?

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Journal Fisheries Research Board Canada

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Le *Style Manual for Biological Journals* (3e éd., publié par l'American Institute of Biological Sciences, 3900 avenue Wisconsin N.O., Washington, D.C.) sert de guide quant à la forme de présentation. Le *Webster's Third New International Dictionary* et le *Grand Larousse Encyclopédique* font autorité pour l'orthographe des mots. Les titres de périodiques sont abrégés suivant les *Biological Abstracts*. Les références bibliographiques dans le texte doivent suivre le système nom de l'auteur-année. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (Troisième édition, 1970), Publication spéciale No. 6 de l'American Fisheries Society.

Les *notes* se distinguent des *articles* par la portée et le degré d'achèvement, plutôt que par la qualité des recherches. Les notes peuvent traiter de problèmes à portée restreinte et facilement définissables; de travaux qui en corroborent d'autres; d'engins et de méthodes de pêche, ou de techniques de recherche; de découvertes dérivées d'une recherche de plus grande envergure; de progrès accomplis dans l'exécution de projets abandonnés; enfin, de résultats préliminaires assez importants pour en justifier la publication avant la solution complète du problème. L'agencement des notes peut être aussi flexible que celui des articles, sauf qu'elles ne doivent pas avoir d'en-têtes de paragraphes centrés. La longueur ne doit pas dépasser quatre pages.

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Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes au but de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou dans le texte même? Est-ce que certaines données devraient être présentées séparément, dans un rapport manuscrit ou dans un dépôt de données? Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la biologie?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le *titre* est-il concis, tout en étant représentatif du contenu du rapport?

Le *résumé* donne-t-il l'essentiel des connaissances nouvelles?

L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème?

La section *matériel et méthode* contient-elle le minimum de détails qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données?

Les généralisations sur les *résultats* sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions?

La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes?

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Guide for Typists Preparing Copy

Read "Guide to Authors" in the current volume of the *Journal*. When in doubt about how to type or arrange details, follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably size 21.5 × 28 cm (8.5 × 11 inches). If possible, use paper with the lines numbered in the margin. Leave all margins at least 2.5 cm wide.

Double-space all parts of the manuscript, including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize only the first word and proper names and adjectives. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numerals. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

On the first page type only the title, the authors' names and affiliations, related footnotes, and the running head (see Appendix A). Type the abstract on a separate page (see Appendix B). Number all pages, beginning with the title page and including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send the ribbon copy and two other clear copies to the Office of the Editor.

Tables: Examine the current volume of the *Journal* to see how tables are set up (see Appendix C).
Note especially the following concerning *numbered tables:*

Type each on a separate page, using paper without the lines numbered.

Number them with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines (see Appendix C).

Illustrations: Send at least 3 *glossy prints* (no larger than 21.5 × 28 cm) of each illustration with the manuscript. Type the author's name and figure number on a strip of paper and fasten it to the back of the print. Do not write or type on the print itself. Also, type the captions in succession on a separate page, headed "Captions for illustrations." Put this page at the end of the manuscript.

Where each figure is first referred to, type in the margin "Fig. — near here."

Mathematical Expressions, Equations, and Formulas: Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (see Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter *l* and the numeral *one*, and between the capital letter *O* and the numeral *zero*. Make other explanatory notes similarly.

References: Check the text to see that all references in the list are referred to. Type the reference list, double-spaced, in the style used in the *Journal* (see Appendix E). Names of journals are abbreviated as in the *Biological Abstracts* list; if an abbreviation is in doubt, type the name in full.

Spellings: About 100 words common in fisheries journals are listed in Appendix F.

Appendices: Appendices A to F are available on request from the Office of the Editor.

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Guide pour les secrétaires d'auteurs

Lisez le "Guide des Auteurs" reproduit dans l'édition courante du *Journal*. Si vous avez des doutes sur la façon de dactylographier le texte ou d'en agencer les détails, suivez la pratique du *Journal*.

Dactylographiez le manuscrit sur papier blanc de bonne qualité, et non sur papier pelure, mesurant de préférence 21.5 × 28 cm (8.5 × 11 pouces), laissant toujours une marge d'au moins 2.5 cm. Si possible, employez un papier avec lignes numérotées en marge.

Tout le manuscrit, y compris tableaux, légendes de figures, renvois et références bibliographiques, devra être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique. Mettez en retrait la première ligne de chaque paragraphe du texte et de chaque renvoi.

Dans les titres et les en-têtes, n'employez la majuscule que pour le premier mot et les noms propres. Pour les petites majuscules, employez les minuscules du dactylographe.

Indiquez tous les renvois du texte par des chiffres arabes suscrits. Numérotez les renvois consécutivement par tout le texte, à commencer par ceux de la page titre. Placez chaque renvoi directement sous sa référence, le séparant du texte par des lignes horizontales.

La première page ne doit contenir que le titre de la publication, le nom et l'affiliation de ou des auteurs, les renvois appropriés et le titre courant (voir Appendice A). Dactylographiez le résumé sur une page séparée (voir Appendice B). Numérotez chaque page, à commencer par la page titre, et y compris celles qui contiennent les tableaux et la légende des figures.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie et ainsi que deux copies lisibles au bureau du Directeur de la publication.

Tableaux. Consultez une copie du *Journal* pour la composition des tableaux (voir Appendice C).

Portez une attention particulière à ce qui suit au sujet des *tableaux numérotés*.

Dactylographiez chaque tableau sur feuille séparée, vous servant de papier sans lignes numérotées.

Numérotez les tableaux en chiffres arabes.

Tracez des lignes horizontales au-dessus et au-dessous des en-têtes et au-dessous des colonnes, rarement ailleurs; ne tracez jamais de lignes verticales; laissez plutôt des espaces supplémentaires.

Indiquez les renvois dans les tableaux par les minuscules suscrites et placez les renvois au bas du tableau.

Placez les tableaux à la suite des références bibliographiques.

A l'endroit où le tableau est mentionné pour la première fois, indiquez dans la marge "Tableau — près d'ici."

Remarquez que les *tableaux dans le texte* ne sont pas numérotés, sont dactylographiés avec le texte et ne requièrent que rarement des lignes horizontales (voir Appendice C).

Figures: Envoyez avec le manuscrit trois photos *sur papier glacé* (21,5 × 28 cm ou moins) pour chaque illustration. Dactylographiez le nom de l'auteur et le numéro de la figure sur une lisière de papier que vous collerez au dos. N'écrivez pas à la main ou à la machine sur la photographie même. En plus, dactylographiez les légendes, dans l'ordre, sur feuille séparée, intitulée "Légendes des figures." Intercalez cette feuille à la suite du texte.

A l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge "Fig. — près d'ici."

Equations, formules et expressions mathématiques: Laissez trois espaces au-dessus et au-dessous des lignes renfermant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous d'équations et de formules. Placez chaque composante des différentes expressions dans la position qui lui est propre (voir Appendice D).

Indiquez clairement tous les symboles. Epelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre *l* et le chiffre *un*, et entre la majuscule *O* et le chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Références: Vérifiez le texte afin de vous assurer que toutes les références apparaissant dans la liste bibliographique sont bien mentionnées dans le texte. Dactylographiez à double interligne dans le style en usage dans le Journal (voir Appendice E). Les noms de revues sont abrégés suivant les *Biological Abstracts*; en cas de doute, écrivez le nom au long.

Orthographe: Une liste d'environ 100 mots communément employés dans les périodiques sur les pêches est donnée en Appendice F.

Appendices: On peut se procurer une copie des Appendices A à F sur demande au bureau du Directeur de la publication.

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BULLETIN 184

(Traduction française du bulletin de W. B. Scott et E. J. Crossman intitulé Freshwater Fishes of Canada publié en 1973.)

Poissons d'eau douce du Canada

W. B. Scott • E. J. Crossman

Depuis nombre d'années se fait sentir un besoin impérieux de réaliser une publication sur l'identification, la distribution, la biologie et l'importance économique des Poissons d'eau douce du Canada. Voici enfin un ouvrage qui traite avec précision de toutes les espèces des eaux douces canadiennes. Les descriptions se fondent sur les examens de spécimens, réalisés expressément pour le travail en question. Dans le cas de nombreuses espèces, les cartes sont les premières présentations graphiques de la répartition de ces Poissons au Canada; la distribution dans le monde est aussi précisée quand l'aire naturelle de l'espèce traverse les frontières canadiennes. Réalisés pour la plupart spécialement pour cet ouvrage, les dessins illustrent, comme point de référence, des exemples types de chaque espèce. Les artistes ont réussi à atteindre un degré de précision et de réalisme exceptionnel. Les clés d'identification des divers Poissons ont fait l'objet d'une mise au point spéciale pour les Poissons du Canada et ont subi des vérifications pendant plus de trois ans. Elles comprennent plus d'un caractère dans chaque cas pour permettre de distinguer tous les Poissons de notre grand pays. Au-delà de 1,400 références et des sections spéciales de lectures suggérées couvrent à peu près tout ce qui a été écrit sur les Poissons d'eau douce du Canada.

For many years there has been an acute need for a publication on the identification, distribution, biology, and economic importance of the freshwater fishes of Canada. This book provides facts and figures on all species occurring in Canadian fresh waters. The descriptions are based on examinations of specimens carried out expressly for the preparation of this book. For many species the maps will be the first graphic presentation of their Canadian range, and the world distribution is given if the natural range extends beyond Canadian boundaries. Most of the drawings were prepared especially for this book, using typical examples of each species for reference. The artists have been unusually successful in achieving a high degree of accuracy and realism. The keys to the identity of the various fishes were prepared specifically for Canadian fishes and have been tested for more than three years. They include more than one character in each choice in an attempt to separate all of the fishes occurring over the whole of such a large country. Over 1400 references and special Suggested Reading sections cover most of the literature on Canadian freshwater fishes.

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BULLETIN 188

Aquaculture in Canada

The practice and the promise

H. R. MacCrimmon • J. E. Stewart • J. R. Brett

Some forms of aquaculture have existed in Canada for many years on a small scale. This Bulletin reviews the current practices and identifies opportunities for establishing a substantial and viable industry based upon freshwater fisheries, marine fishes, and invertebrates. It focuses on the scientific and technical basis for such an industry and on the constraints to be encountered, and identifies areas that need experimental development to provide pilot-scale production data and economic assessments.

L'aquiculture, sous une forme ou sous une autre, existe au Canada depuis plusieurs années. Cet ouvrage fait la revue des pratiques courantes et signale les occasions d'établir une industrie substantielle et viable, fondée sur les pêches d'eau douce, les poissons de mer et les invertébrés. Il se concentre sur les bases scientifique et technique d'une telle industrie, de même que sur les contraintes à affronter, et identifie les domaines qui requièrent un développement expérimental, en vue d'obtenir des données sur une production à l'échelle pilote et des évaluations de rentabilité.

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Journal of the Fisheries Research Board of Canada

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